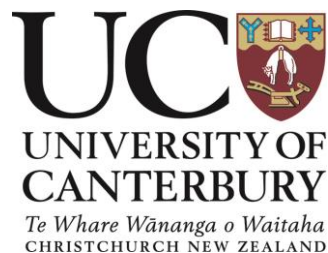


# Early life history dynamics of the New Zealand whitebait species

A thesis submitted in partial fulfillment  
of the requirements for the Degree  
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Georgia Jean McClintock

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## Abstract

In New Zealand, ‘whitebaiting’ describes a nationwide recreational and commercial fishery that is of high cultural significance. The New Zealand whitebait fishery is comprised predominantly of five diadromous galaxiid species, īnanga (*Galaxias maculatus*), kōaro (*G. brevipinnis*), banded kōkopu (*G. brevipinnis*), giant kōkopu (*G. argenteus*) and shortjaw kōkopu (*G. postvectis*). In recent years, four out of the five whitebait species have been listed as ‘declining’ or ‘threatened’ in large part due to increased stressors such as habitat degradation. The whitebait fishery is governed by regulations that were set 20 years ago and management is separated into two spatial units: the West Coast of the South Island and the rest of New Zealand.

With the increasing recognition that restricted connectivity is driving local adaptation in a large number of marine species, this study investigated possible local adaptations in early life history traits of the five whitebait species. To provide insight into what is occurring at sea, the age at migration and daily pelagic growth rate of post-larvae were compared across broad spatial and temporal scales. Whitebait were sampled from 26 rivers within nine regions of New Zealand during September-December 2015. From these samples, a total of 1567 whitebait were aged by counting daily rings in their otoliths: īnanga (n=794), kōaro (n=296), banded kōkopu (n=446), giant kōkopu (n=30) and shortjaw kōkopu (n=2).

Strong spatial trends in age at migration and daily pelagic growth were seen in four whitebait species (īnanga, kōaro, banded kōkopu and giant kōkopu). At lower latitudes of New Zealand (North Island) whitebait entering rivers were on average younger with higher levels of average daily pelagic growth. At higher latitudes (South Island) whitebait were older with lower growth rates. Additionally, whitebait on the east coast of the South Island tended to be older with lower growth rates than those on the west coast at similar latitudes.

Age at migration decreased and average daily pelagic growth increased between months for īnanga (September- November) and banded kōkopu whitebait (September- December) in most regions. However, in other regions the age of whitebait increased during the settlement with concomitant reductions in growth or did not vary significantly.

Back-calculated hatch dates of īnanga and kōaro whitebait had broad distributions from May until August. Banded kōkopu and giant kōkopu whitebait hatch dates had a narrower, unimodal distribution and the majority of banded kōkopu hatched during June and July. Giant kōkopu whitebait hatched later, predominately during July and August.

This study is the first to make broad-scale spatial comparisons of age and growth of the five whitebait species. From the findings it is apparent that the New Zealand whitebait fishery is not comprised of a single meta-population and that spatial differences in oceanic conditions drive local adaptation and variability in early life history traits.

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I hope you enjoy it.

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## Chapter 1: General Introduction and Methodology

### 1.1 General introduction

#### 1.1.1 An overview of global fish stocks

Marine and freshwater fisheries are a vital source of food, nutrition, livelihood and income for hundreds of millions of people around the world. For centuries, our oceans and freshwater catchments were considered an abundant food source, but many are now being pushed or have already been pushed towards the point of collapse. Global trends show that since 1990 approximately one quarter of the world's marine fish stocks have been over-exploited, depleted or are recovering from depletion (17%, 7% and 1% respectively) (Beddington, Agnew and Clark, 2007). The Northeast and Northwest Atlantic, the Mediterranean and the Black Seas have been recorded as the areas with the largest numbers of depleted stocks (Beddington *et al.*, 2007, Pauly *et al.*, 2002). It is now suggested that up to 70% of global marine fish stocks are overexploited due to stressors such as overfishing, habitat change and pollution (Branch *et al.*, 2011).

Global trends for freshwater species have found a 50% reduction in species index from 1970 to 2000, with the extinction of 91 freshwater fish species documented within the last century (Loh and Wackernagel, 2004). Qualitative data for freshwater biodiversity have also documented trends in population declines, with 54% of freshwater vertebrates exhibiting a decline, with a tendency toward higher values in tropical latitudes (Dudgeon *et al.*, 2006). Furthermore, 32% of the world's amphibian species are now threatened with extinction, while birds and mammals face 12% and 23% respectively (Dudgeon *et al.*, 2006).

So what is causing this shift from an abundant food source to two of the most endangered ecosystems in the world? For freshwater, the main threats to biodiversity can be grouped into five interacting categories: overexploitation; water pollution; degradation or destruction of habitat, flow modification and invasion of non-indigenous species (Allan and Flecker, 1993, Jackson *et al.*, 2001, Revenga *et al.*, 2005, Dudgeon *et al.*, 2006). Dudgeon *et al.* (2006) suggested that freshwater systems are susceptible to these threats because of the “disproportionate richness of inland waters as a habitat for plants and animals”. Freshwater habitats contain only 0.01% of the world's water and only cover 0.08% of the earth's surface, but contain roughly 100,000 species (Gleick, 1996, Lundberg *et al.*, 2000). In New Zealand,

these five main threats and the negative impacts they have on freshwater habitats and associated species are increasingly documented (Ryan, 1991, Townsend, 1996, Quinn *et al.*, 1997). It is estimated that 67% of native freshwater and estuarine taxa are now considered threatened or at risk (Allibone *et al.*, 2010). Although conservation efforts such as habitat restoration have been shown to improve biodiversity in degraded freshwater catchments (Parkyn *et al.*, 2003), species such as longfin eel (*Anguilla dieffenbachii*) and galaxiids that comprise the whitebait fishery are still displaying trends of decline (Allibone *et al.*, 2010).

### 1.1.2 What is whitebait?

Whitebait is the collective term used around the world for small juvenile fish that are caught and consumed in large numbers (McDowall, 1968). In New Zealand ‘whitebait’ describes a nationwide recreational and commercial fishery in which large shoals of post-larval fish are caught as they migrate from coastal waters into freshwater catchments. These shoals are composed of multiple species that are characterized as slender and transparent in appearance and range from 40-60 mm in total length (McDowall, 1964). Predominantly, the shoals are fish that belong to the Galaxiidae family, although other families, for example smelt (Retropinnidae) and eels (Anguillidae), are occasionally documented (McDowall, 1964). Overall this New Zealand fishery is of high cultural and economic value, with prices reaching up to \$100 per kg (McDowall and Eldon, 1980).

The Galaxiidae are the most widely distributed freshwater fish family in the southern hemisphere, occurring in New Zealand, Australia, South Africa, Chile and Argentina (McDowall, 1964). New Zealand is home to 26 galaxiid species, five of which have been found in the whitebait catch. These five species are the only species in the genera known to be diadromous (i.e., migrate between marine and freshwater catchments) (McDowall, 1964, McDowall, 1968, McDowall and Eldon, 1980). The species are: īnanga (*Galaxias maculatus*), kōaro (*G. brevipinnis*), banded kōkopu (*G. fasciatus*), shortjaw kōkopu (*G. postvectis*) and Giant kōkopu (*G. argenteus*) (McDowall and Eldon, 1980, Baker and Hicks, 2003).

#### Īnanga (*Galaxias maculatus*)

Īnanga is the predominant species found in catches of whitebait. It is a lowland species with poor climbing ability (Baker and Hicks, 2003). It is less selective for habitat and therefore

occupies a diverse range of streams and rivers. The species is small and short-lived with most individuals having a life span of only one year. Individuals can grow to 120 mm in length.

#### Kōaro (*G. brevipinnis*)

This species is unique through its ability to climb. It is found in selective habitats that consist of fast-flowing, clear and forested streams. Being a good climber allows them to travel further upstream in comparison to other species. This species has been documented living up to 15 years or more and commonly grow to lengths between 160-180 mm (Baker and Hicks, 2003).

#### Banded kōkopu (*G. fasciatus*)

This species is a good climber and has been found up to 550 m above sea level and commonly growing up to 200 mm in length. They reside in pools that have overhanging banks, logs and boulders. They require bankside vegetation for survival as they feed on insects falling from overhanging plants (Richardson, Rowe and Smith, 2001).

#### Shortjaw kōkopu (*G. postvectis*)

This is a rare and seldom documented species. Those that have been captured were found inhabiting low to moderate elevations. They are extremely selective in habitat preference requiring the presence of boulders and forested streams in order to survive. They are recorded to grow to a length of 150 to 200 mm and are endemic to New Zealand (McDowall, 1984).

#### Giant kōkopu (*G. argenteus*)

As their common name suggests, this is the largest of the galaxiids, reaching between 300 and 400 mm. They inhabit wetlands, lakes and forested streams near sea level as a result of their poor climbing ability (McDowall and Kelly, 1999, Bonnett and Sykes, 2002). They are a slow-growing, long-lived species; a large individual was estimated to be 21-27 years old from otolith growth rings (McDowall, 1990).

### 1.1.3 Whitebait life cycle

The five species of galaxiids that make up the New Zealand whitebait fishery are diadromous. The term diadromy and subcategories anadromy, catadromy and amphidromy were first described by Myers (1949) to categorise fish that migrate between marine and freshwater biomes at various life stages. Myer's definitions were as follows: diadromous -

truly migratory fishes that migrate between sea and freshwater; anadromous - fishes that spend most of their lives in the sea and that migrate to freshwater to breed; catadromous – fishes that spend most of their lives in freshwater and that migrate to sea to breed; and amphidromous - fishes whose migration from fresh water to sea, or vice-versa, is not for the purpose of breeding but occurs regularly at some other stage of the life cycle (McDowall, 1992).

New Zealand whitebait fall under the amphidromy subcategory, where eggs hatch in freshwater, larvae migrate to sea where they remain for several months, before returning to freshwater catchments where they move upstream to grow, reach sexual maturation and reproduce (McDowall and Kelly, 1999). Although the five whitebait species are amphidromous, their spawning methods and habitat vary considerably, but little is known about the reproduction of most of the species (McDowall, Mitchell and Brothers, 1994). *Īnanga* is an annual, semelparous species where spawning is based on lunar and tidal rhythms. Eggs are deposited supratidally during spring tides in upper estuarine areas. The eggs adhere to the stems and aerial root-mats of riparian vegetation (Hickford and Schiel, 2011a). *Īnanga* egg development takes approximately 28 days, until the next set of spring tides when re-immersion of eggs occurs and the newly-hatched larvae are washed out to sea (McDowall, 1968).

Little is known about the spawning biology of the remaining diadromous galaxiid species but it is believed that spawning takes place between autumn and winter in freshwater biomes. Banded kōkopu spawning has been observed more frequently, where eggs are deposited in winter amongst bank vegetation (Mitchell and Penlington, 1982, McDowall and Kelly, 1999). Kōaro and shortjaw kōkopu spawning sites have been documented in autumn and winter in Katikara Stream (Taranaki) where eggs were partially submerged on bankside vegetation (Allibone and Caskey, 2000, Charteris, Allibone and Death, 2003). Giant kōkopu spawning has only recently been described, but follows a similar spawning strategy to the other whitebait species. Spawning takes place during the winter months where eggs are deposited supratidally during spring tides. Egg development then takes place in terrestrial habitats before being re-submerged in water and hatching (Franklin *et al.*, 2015).

Although spawning behaviour and habitat vary between the five whitebait species, all go to sea for pelagic development soon after hatching. During the pelagic phase, their location and

distance from land is largely unknown (McDowall *et al.*, 1994). Post-larval juveniles return to rivers in large mixed species shoals by sensing freshwater plumes, usually following large rain events (McDowall and Eldon, 1980, Hickford and Schiel, 2011b). It is during this life stage that commercial and recreational fishers harvest whitebait. Those that are not caught migrate upstream where they grow and mature, before moving to spawning sites.

#### **1.1.4 Anthropogenic effects on whitebait species**

For many years, commercial and recreational fisherman have speculated that post-larval numbers are declining, but there was little specific documentation that could back the claims. Nevertheless, reviews conducted by Allibone *et al.* (2010) and Goodman *et al.* (2014) have concluded there is a decline in adult whitebait numbers. From the five whitebait species, three are now listed as ‘declining’ and one is ‘threatened’ nationally. Anthropogenic activities are largely to blame due to the degradation of New Zealand water quality and reduction of surrounding habitat (Miller, Williams and Williams, 1989). In the last century, New Zealand has seen increased installments of dams, weirs and culverts, larger inputs of pollution, increased water extraction for irrigation, influxes of invasive species and loss of riparian and in-stream habitat. This transition from undisturbed to human-dominated landscapes has been shown to heavily influence surrounding ecosystems (Allan, 2004).

The introduction of dams, weirs and culverts has played a key role in human expansion by regulating river systems to generate electricity, providing irrigation to pastures and allowing access to areas separated by freshwater catchments (Jellyman and Harding, 2012). However, these types of infrastructures, commonly lead directly to changes to flow, severed migratory pathways, altered disturbance regimes, decreased downstream sediment transport and sizeable changes to the physical, chemical and biological processes within freshwater ecosystems (Ward and Stanford, 1983, Young, Smart and Harding, 2004, Jellyman and Harding, 2012). For many of New Zealand’s freshwater fish and invertebrates these changes have had large negative effects (Nicola, Elvira and ALMooovAR, 1996, Santucci, Gephard and Pescitelli, 2005). For whitebait returning from sea, the need for access to upstream adult habitat is crucial for maintenance of populations. Dams and culverts sever the migratory pathway necessary for the life cycle of whitebait, restricting access to adult habitat and spawning grounds (McDowall, 1998, Leathwick *et al.*, 2008, Doehring, Young and McIntosh, 2012). Degradation or loss of access to these important, stage-specific habitats has



been shown to create source-sink populations in īnanga, which commonly leads to demographic deficits and population bottlenecks (Hickford and Schiel, 2011a).

Altered flow regimes are thought to be another driver of adult whitebait population declines. Galaxiids feed on invertebrate drift with adequate flow needed to provide sufficient food supply (Main and Winterbourn, 1987, Jowett, 2002). Īnanga feed on drifting invertebrates and prefer low velocity locations ( $0.03\text{--}0.07\text{ ms}^{-1}$ ), but anthropogenic activities such as culverts channelise water and increase velocity in surrounding areas. Water extraction slows flows and likely disrupts feeding capabilities (McDowall *et al.*, 1996).

Agricultural land use has been shown to negatively affect water quality by introducing diffuse inputs of pollutants and pesticides and increasing levels of sediments and nutrients within the water column (Cooper, 1993). Suspended sediment increases turbidity and eventually reduces fish abundances (Ryan, 1991, Richardson and Jowett, 2002). Increased nutrients can push freshwater catchments to a eutrophic state which in turn can cause loss of amenities and services provided by freshwater systems (Smith, 2003).

Increased grazing has been widely documented to affect riparian vegetation and in-stream channel flows (Allan, 2004). Important influences of the riparian zone include thermal buffering, provision of shade, nutrient interception, bank stability and, most importantly for the whitebait species, the provision of coarse woody material for habitat and spawning (Omernik, Abernathy and Male, 1981, Crook and Robertson, 1999). An increase in agricultural activities and intensified grazing has led in some cases to the complete loss of the riparian zone surrounding freshwater catchments. The nature and composition of riparian vegetation can be closely associated with spawning success along with abiotic conditions such as height, density, humidity and temperature of surrounding vegetation (Hickford and Schiel, 2011a). A study by Hickford and Schiel (2011a) found that īnanga favoured egg deposition in the common riparian species *Schedonorus phoenix*, *Agrostis stolonifera* and *Juncus edgariae*, with the survival of eggs increasing exponentially as these species increased in cover. The study also found higher temperatures and less humid conditions in riparian areas that were exposed to agricultural grazing, with overall egg densities in ungrazed plots being up to 10 times higher than in grazed plots.

The widespread negative effects of introduced fish species, such as trout on galaxiids were first described by Townsend and Crowl (1991). Although it was documented in 1928 by Hope that whitebait are prey to multiple species of fish and birds, both indigenous and non-indigenous, Townsend and Crowl (1991) were the first to distinguish between predation and other likely variables causing decline, such as habitat degradation. They showed that trout heavily prey on galaxiid species with very little to no co-occurrence of the two groups in many of our freshwater catchments. The only determinant of co-occurrence was the presence of physical barriers such as waterfalls between the two groups leading to the conclusion that trout likely contribute to the decline and fragmentation of galaxiid populations. Likewise, whitebait mortality by the introduced fish species *Gambusia affinis* was higher in shallow warmer waters, disrupting the distribution of īnanga by displacing them into deeper freshwater habitats (Rowe, Smith and Baker, 2007).

Native fish have also been shown to decrease whitebait numbers. The complete loss of kōaro after the introduction of smelt (*Retropinna retropinna*) into Lake Rotopounamu showed the predation of 2 + year old smelt on juvenile kōaro was sufficient to exclude them from the lake (Rowe, 1993).

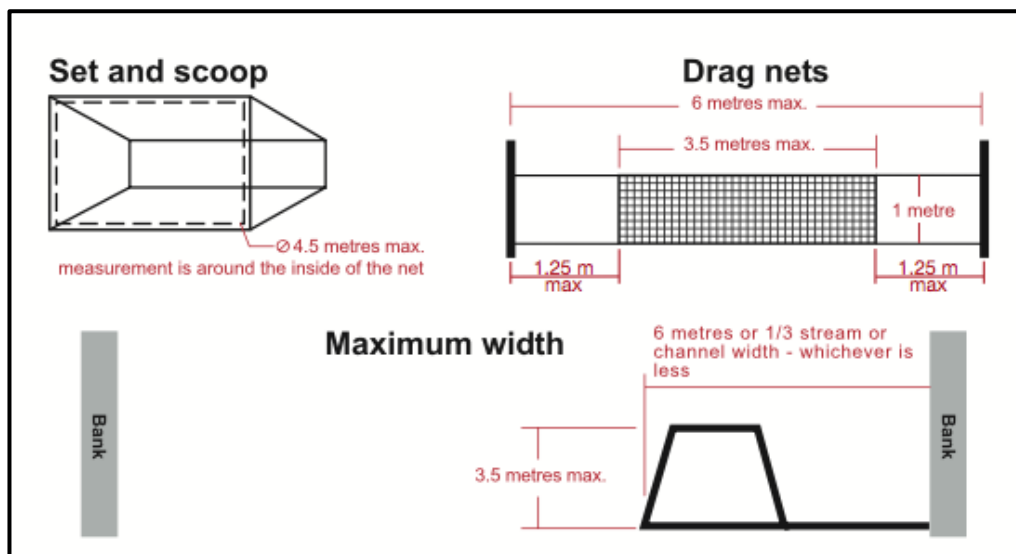
### **1.1.5 Whitebait fishery management**

The New Zealand whitebait fishery has a series of characteristics that together make it unique, but that pose many problems for the management of the species. The whitebait fishery is comprised of several species, some more prevalent than others (McDowall and Eldon, 1980). They are exploited at only one stage of their life cycle when they are post-larval fish migrating from sea to freshwater and those that escape fishing nets are not targeted by fishermen again. The post-larval fish that are caught for consumption are never given the chance to reach sexual maturity and reproduce which makes the whitebait fishery distinct from most other fisheries (McDowall and Eldon, 1980).

The responsibility of managing the fishery was assigned to the Department of Conservation (DOC) in 1990 when they were given a mandate for preservation of indigenous flora and fauna (with the exception of commercial fisheries) in New Zealand. Under the Conservation Act 1987 sections 6a and b, DOC was asked to “preserve, so far as is practicable, all indigenous freshwater fisheries, and protect recreational freshwater fisheries and freshwater fish habitats”. The Whitebait Regulations (1994) Fisheries Act set basic national rules:

fishing is permitted only between 5:00 am and 8:00 pm, or during New Zealand Daylight Saving time between 6:00 am and 9:00 pm. Netting restrictions include using only a single whitebait net that must not (Fig. 1.1):

- Have a mouth larger than 4.5 m measured on the inside of the net
- Have framing material larger than 120 mm
- Be longer than 3.5 m in length
- Exceed more than 1/3 of the water channel width (including screens), or be used in conjunction with another person's net.



**Figure 1.1.** Set, scoop and drag net restrictions and regulations for the New Zealand whitebait fishery. Image source: <http://www.doc.govt.nz/whitebait>.

The New Zealand whitebait fishery is also controlled by seasons. The West Coast of the South Island's season runs from 1 September - 14 November while the rest of New Zealand's is 15 August - 30 November. The whitebait fishery is managed as one population. However, measures were taken in 1994 to adjust the whitebaiting season for the West Coast of the South Island to allow less common species such as giant kōkopu access to upstream habitats (McDowall and Kelly, 1999).

When comparing the New Zealand whitebait fishery to additional fisheries governed by New Zealand, there are clear differences in management techniques. For example, New Zealand snapper (*Pagrus auratus*) is one of New Zealand's most popular recreational fisheries. Management of the fishery is split into seven management areas, with catch allowances and

size limits set differently for each area depending on population health. Annual harvest surveys, periodic stock assessments and background knowledge all contribute to the effective management of the fishery. Annual fisheries harvest is quantified by onsite surveys, offsite regional telephone and diary surveys, and aerial-access onsite monitoring (ramp and vessel activity in water). Stock assessments use commercial data and trawl data to measure an array of demographics such as age and length. Background knowledge such as water temperature, recruitment success and geographical variation in growth is reflected in the snapper fishery management (Francis, 1993) (<https://fs.fish.govt.nz>).

The snapper fishery has shown an increase in spawning stock since 1990 and it is clear that a broad understanding of the species and regular stock surveying are key to effective management of the species (Hauser *et al.*, 2002). By comparison, the whitebait fishery imposes very few regulations. No license is needed, no quota on total weight of catch is set and there is no annual adjustment to regulations in response to the health or otherwise of the fishery. There are no dedicated stock monitoring tools, comprehensive catch data or broad scale studies that can provide insight into how whitebait varies across New Zealand and how stocks are performing.

Historical research of the whitebait fishery has formed the basis for the management regulations set today. Studies by McDowall, Robertson and Saito (1975), McDowall and Eldon (1980) and McDowall *et al.* (1994) were among the first to describe post-larval whitebait where life history traits such as the age, size and composition of migrating shoals were defined. Although these studies provided valuable information on the fishery, all have been done at a small spatial scale. For example, McDowall *et al.* (1994) aged the five whitebait species from seven rivers from the North Island and three from the South Island and used this information to make generalisations about the entire fishery. Widespread species such as galaxiids, are likely exposed to differing localised conditions and have shown to exhibit variable life histories as a response (Egan, 2017). Therefore, applying uniform population models and management strategies to such a species can be ineffective (Barbee *et al.*, 2011) ( See Chapter 2, Section 2.2).

Modern studies have begun to recognise variability within the whitebait fishery and are incorporating spatial and temporal components into their research. Examples include a study by Egan (2017), where the migratory dynamics and early life history traits of īnanga were

examined. Sampling took place across four regions of New Zealand with samples taken from up to three rivers within each region. Findings indicated larger-scale spatial and temporal processes drove the variation exhibited in migratory characteristics such as size, age, condition and hatch dates of post-larvae whitebait. Yungnickel (2017) conducted an even broader scale study, which incorporated 15 regions of New Zealand with 92 rivers sampled for whitebait. The study found substantial spatial and temporal variation in the species composition of the whitebait catch. Additionally, timing of banded kōkopu and giant kōkopu whitebait migrations were found to be earlier in the North Island than the South Island.

The spatial and temporal variances evident within the whitebait fishery suggest the fishery is not composed of one population. To effectively manage the whitebait fishery, understanding how spatial and temporal processes drive variation within the five whitebait species is crucial. Variations in early life history traits such as differing age classes, have been shown to give rise to different phenotypes that differ in body size, behaviour, sex ratio and reproductive success (Garcia de Leaniz *et al.*, 2007). Furthermore, growth rates during the pelagic larval phase can influence the maturity schedules of adult fish, where fish exhibiting faster growth reach sexual maturity sooner (Brophy and Danilowicz, 2003). Knowledge of how spatial and temporal processes affect whitebait populations will fill the gaps of what goes on during pelagic larval duration, inform the possible legacy effects that will be expressed in adult individuals, and disentangle historical research on hatch-date distributions.

This study is structured to use samples of multiple rivers in different regions around New Zealand to understand how spatial and temporal processes drive variation in early life history traits in the five whitebait species. Although studies have examined early life history traits in these whitebait species before, few have examined how traits have varied within and among regions of New Zealand.

### **1.1.6 Objectives and hypotheses**

The objectives of this thesis are to expand on the current knowledge of age and growth data for the five species of diadromous galaxiids that make up the whitebait catch. Particular emphasis will be placed on īnanga, but the remaining species will also be examined. In Chapter 2, I examine the spatial differences in age of īnanga whitebait throughout regions of New Zealand within multiple freshwater catchments. In Chapter 3, I examine the temporal changes in age over the months September through to November of īnanga whitebait

throughout regions of New Zealand. For Chapter 4, I examine spatial and temporal changes in age of whitebait of the remaining four species of diadromous galaxiids throughout New Zealand. And finally, Chapter 5 is the general discussion.

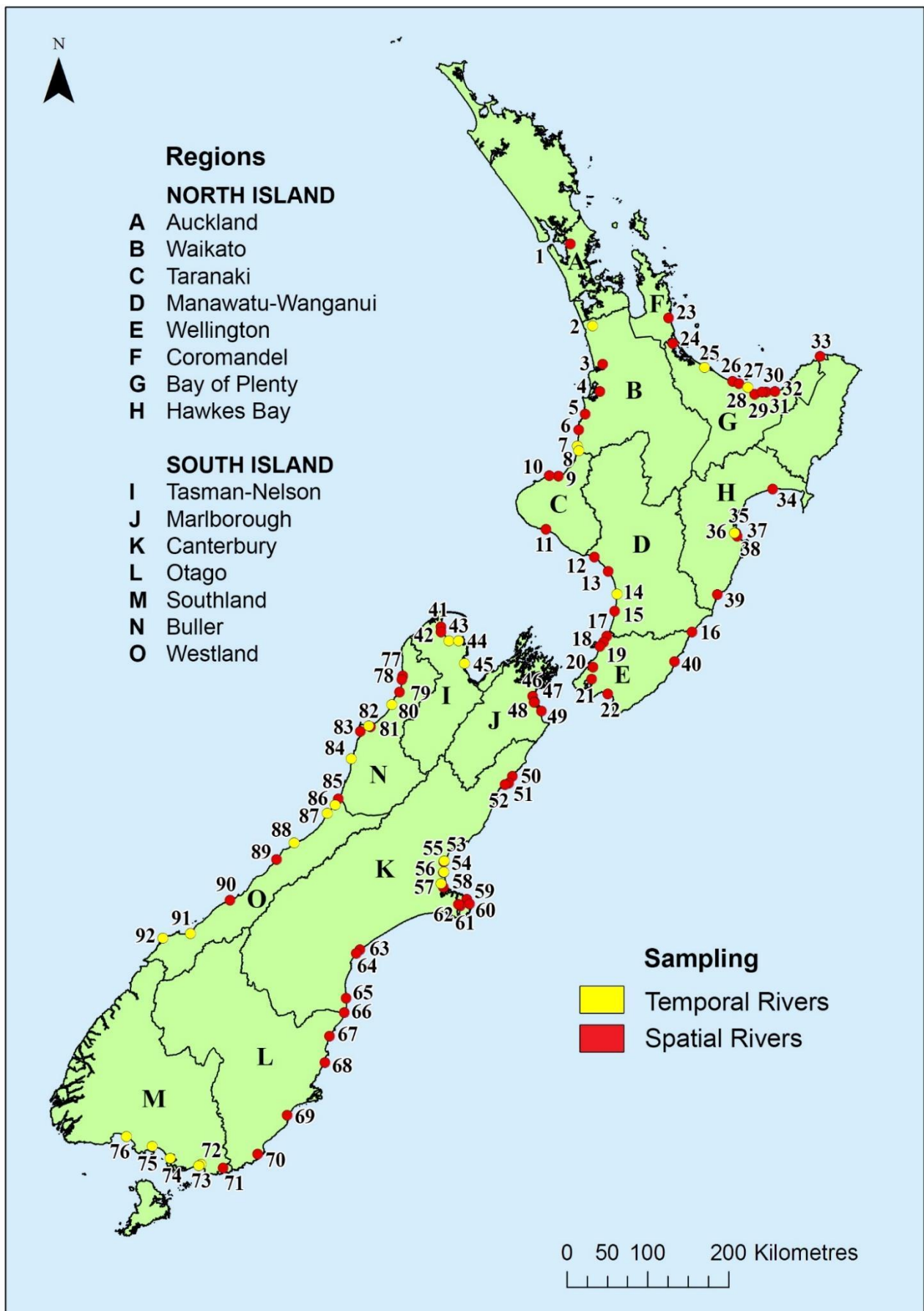
## **1.2 Collection methodology**

### **1.2.1 Study design**

Whitebait collection took place in 2015 and 2016 by Mark Yungnickel, a previous M.Sc. student at the University of Canterbury (Yungnickel, 2017).

Whitebait were collected over the two-year period by members of the University of Canterbury's Marine Ecology Research Group, experienced whitebaiters, the Department of Conservation and regional councils. The sampling design included spatial and temporal components. Spatial sampling included multiple rivers within varying regions of New Zealand. Temporal sampling took place within these regions before, during and after the whitebait season. A total of 92 rivers and streams were sampled during 2015 with sampling commencing 1 July and completed roughly every two weeks until 31 December 2015. During 2016 only a subset (eight) rivers were sampled again during the whitebait season (Fig. 1.2, Table 1.1). Sampling completed outside of the whitebait season was undertaken with a research permit from the Department of Conservation (44336-FAU).

From the original collection of samples, only a subset of regions, rivers and dates were used for the purpose of my study due to time constraints and set objectives.



**Figure 1.2.** The 92 whitebaiting rivers sampled throughout New Zealand during 2015 and 2016 for Mark Yungnickel's research.

**Table 1.1** Whitebaiting rivers sampled throughout New Zealand for Mark Yungnickel’s 2015 study. River numbers and sampling undertaken shown in Fig. 1.2.

Region	River	River Number	Sampling Undertaken	Region	River	River Number	Sampling Undertaken
Auckland	Hoteo River	1	Spatial	Bay of Plenty	Tarawera River	26	Spatial
Waikato	Waikato River	2	Temporal		Rangitāiki River	27	Spatial
	Waingaro River	3	Spatial		Whakatāne River	28	Temporal
	Oparau River	4	Spatial		Nukuhou River	29	Spatial
	Marokopa River	5	Spatial		Otara River	30	Spatial
	Waikawau River	6	Spatial		Waiaua River	31	Spatial
	Awakino River	7	Temporal		Waiotahi River	32	Spatial
	Mokau River	8	Temporal		Whangaparaoa River	33	Spatial
Taranaki	Onearo River	9	Spatial	Hawkes Bay	Wairoa River	34	Spatial
	Waitara River	10	Spatial		Ngaruroro River, Tutaekuri River and Clive River (Mouths)	35	Spatial
	Waingongoro River	11	Spatial		Tūtaekurī River	36	Temporal
Manawatu-Wanganui	Kai Iwi Stream	12	Spatial		Clive River	37	Spatial
	Whangaehu River	13	Spatial		Tutituki River	38	Spatial
	Rangitikei River	14	Spatial		Pōrangahau River	39	Spatial
	Manawatu River	15	Spatial	Wairarapa	Whareama River	40	Spatial
	Owahanga River	16	Spatial	Tasman- Nelson	Aorere River	41	Spatial
Wellington	Otaki River	17	Spatial		Parapara River	42	Spatial
	Peka Peka Stream	18	Spatial		Takaka River	43	Temporal
	Waikanae River	19	Spatial		Wainui River	44	Temporal
	Pauahatanui Stream	20	Spatial		Motueka River	45	Spatial
	Hutt River	21	Spatial	Marlborough	Wairau River Diversion	46	Temporal
	Ruamāhanga River (lake Ferry)	22	Spatial		Wairau River	47	Spatial
Coromandel	Wentworth River	23	Spatial		Opawa River	48	Spatial
Bay of Plenty	Tuapiro Creek	24	Spatial		Awatere River	49	Spatial
	Kaituna River	25	Temporal	Canterbury	Hāpuku River	50	Spatial



**Table 1.1.** Continued.

Region	River	River Number	Sampling Undertaken	Region	River	River Number	Sampling Undertaken
Canterbury	Lyell Creek	51	Spatial	Southland	Waiau River	76	Temporal
	Kowhai River	52	Temporal	Buller	Oparara River	77	Spatial
	Saltwater Creek	53	Spatial		Karamea River	78	Spatial
	Ashley River	54	Spatial		Little Wanganui River	79	Spatial
	Waimakariri River	55	Spatial		Mokihinui River	80	Temporal
	Styx River	56	Spatial		Orowaiti River	81	Spatial
	Avon River	57	Spatial		Buller River	82	Spatial
	Heathcote River	58	Spatial		Okari River	83	Temporal
	Opapa Stream	59	Temporal		Punakaiki river	84	Temporal
	Le Bons Stream	60	Spatial	Westland	Taramakau River	85	Spatial
	Robinsons Stream	61	Temporal		Waimea Creek	86	Temporal
	Pawsons Stream	62	Spatial		Hokitika River	87	Temporal
	Orari River	63	Temporal		Wanganui River	88	Temporal
	Ōpihi River	64	Spatial		Okarito River	89	Spatial
	Waihao River	65	Spatial		Paringa River	90	Spatial
Otago	Waitaki River	66	Spatial		Waiatoto River	91	Temporal
	Kakanui River	67	Spatial		Cascade River	92	Temporal
	Shag River	68	Spatial				
	Taeri River	69	Spatial				
	Owaka River	70	Spatial				
Southland	Waikawa River	71	Spatial				
	Titiroa River	72	Temporal				
	Mataura River	73	Temporal				
	Oreti River	74	Temporal				
	Aparima River	75	Temporal				

### 1.2.2 Study sites

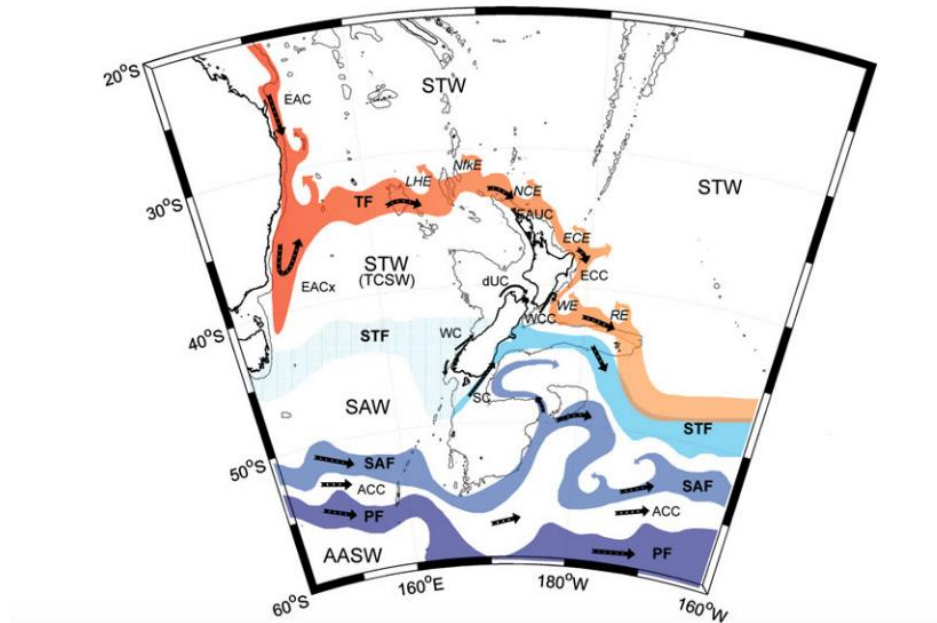
New Zealand is split into three main islands that span 13° of latitude. Its position in the mid-latitudes of the Southern Hemisphere mean land masses span from a subtropical north (34.5° S) to the cool, temperate south (47.5° S) (Schiel, 2004). New Zealand is unique in that its position largely influences the oceanic conditions and climate as a result of complex hydrography (Hurst *et al.*, 2012). Along the mainland the average annual sea surface temperature (SST) varies from 17.5 °C in the far north to 11.5 °C at the southern tip of the South Island, with little variation between the east and west coast (Schiel, 2004).

Hydrographically, New Zealand is surrounded by several distinct water masses: surface subtropical and subantarctic waters; and from the surface down, Antarctic Intermediate Water, Deep Water and Antarctic Bottom Water. The overall movement of water around New Zealand can be split into five main currents. In the North Island, the East Auckland Current and the East Cape Current. Flows between the North and South Islands include the D'Urville Current and flows encompassing the South Island are the Southland and Westland Current (Fig. 1.3). (Heath, 1972, Schiel, 2004, Chiswell *et al.*, 2015). Each oceanic current has varying physical properties such as salinity, temperature and productivity. Overall the highest productivity (chlorophyll- $\alpha$  levels) occurs off the southern region of the South Island and to the east along the continental shelf. This is the result of warmer, nutrient poor, coastal waters mixing with macronutrient-rich and subantarctic waters (Murphy *et al.*, 2001).

To gain a fair representation of the New Zealand whitebait fishery, samples containing spatial and temporal components were used. Overall, samples were collected from eight regions of New Zealand and, where applicable, multiple rivers within each region were sampled. Samples were collected at the beginning of each month on a monthly basis over September through to December.

#### *Waikato*

The Waikato region is located along the west coast of the North Island. This region tends to have humid, warm summers and mild winters with defined seasonal rainfall. Waikato is exposed to prevailing northerly or westerly winds. Chlorophyll- $\alpha$  abundance is consistent with the 'spring bloom cycle' where increased wind-mixing carries the pycnocline below the photo depth leading to enrichment of the photic zone with nitrate concentrations (Murphy *et al.*, 2001). Mean SST ranges from 20.5 °C in summer to 15 °C in winter.



**Figure 1.3.** Surface circulation around New Zealand based on drifter and hydrographic data. Regions of flow are shown as coloured streams. Colours reflect the temperature of the flows with red being warmest, and dark blue being coldest. The STF in the Tasman Sea is density compensated with little flow, as indicated by the shading. Water Masses are Subtropical Water (STW), Tasman Sea Central Water (TSCW), Subantarctic Water (SAW) and Antarctic Surface Water (AASW). Ocean fronts are Tasman Front (TF), Subtropical Front (STF), Subantarctic Front (SAF) and Polar Front (PF). Ocean currents are East Australia Current (EAC), East Australia Current extension (EACx), East Auckland Current (EAUC), East Cape Current (ECC), d'Urville Current (dUC), Wairarapa Coastal Current (WCC), Westland Current (WC), Southland Current (SC) and Antarctic Circumpolar Current (ACC). Eddies are Lord Howe Eddy (LHE), Norfolk Eddy (NfE), North Cape Eddy (NCE), East Cape Eddy (ECE), Wairarapa Eddy (WE) and Rekohu Eddy (RE). (Chiswell *et al.*, 2015).

### *Manawatu*

Migratory anticyclones dominate weather in the Manawatu region. On average, Manawatu is one of the driest regions in the North Island, with coastal areas receiving less than 900 mm of rainfall per year (Chappell, 2015). Chlorophyll- $\alpha$  abundance follows the 'spring bloom cycle' and SST ranges from 18 °C in summer to 14 °C in winter.

### *Bay of Plenty*

The Bay of Plenty is segregated from other regions sampled in the study. Its sheltered shores are swept by the East Auckland Current which produces the warmest seas around New Zealand. Prevailing winds cause upwelling at the shelf edge providing nutrient-rich waters (Sutton and Roemmich, 2001). Sea surface temperature is 19.8 °C on average during the summer months and 16.4 °C during winter.

### *Tasman Nelson*

The Tasman Nelson region has a mild climate with a topography that shelters the region from prevailing winds. The Tasman Bays are bathed in waters originating from the Westland and D'Urville Currents that are relatively warm and nutrient-rich (Heath, 1972). On average, coastal SST ranges from 18 °C in summer to 12.1 °C in winter (Macara, 2012a).

### *Canterbury*

The Canterbury region is characterised by cool, dry conditions (Schiel, 2004). Oceanic flows in the Canterbury region are dominated by the Southland Current. The Southland Current is heavily associated with the Subtropical Front (STF), which consists of warmer, Subtropical Waters (STF), and colder, Subantarctic Waters (SAW). On average, SST ranges from 15 °C in summer to 10.5 °C in winter (<https://www.seatemperature.org/>). Overall, chlorophyll- $\alpha$  production within the region is lowest in winter and highest late summer/early autumn, average production is c. 0.6 mgm<sup>-3</sup> (Murphy *et al.*, 2001).

### *Southland*

Southland is both the most southerly and westerly region sampled in New Zealand, making it the first region to be influenced by weather systems moving in from the west or the South (Macara, 2012b). The Subtropical Front is the predominant oceanographic feature which advects warm, salty subtropical water (Heath, 1972). In summer, SST on average is 15 °C and a cool 10 °C in winter (Heath, 1972). Overall productivity is highest in these waters.

### *Buller*

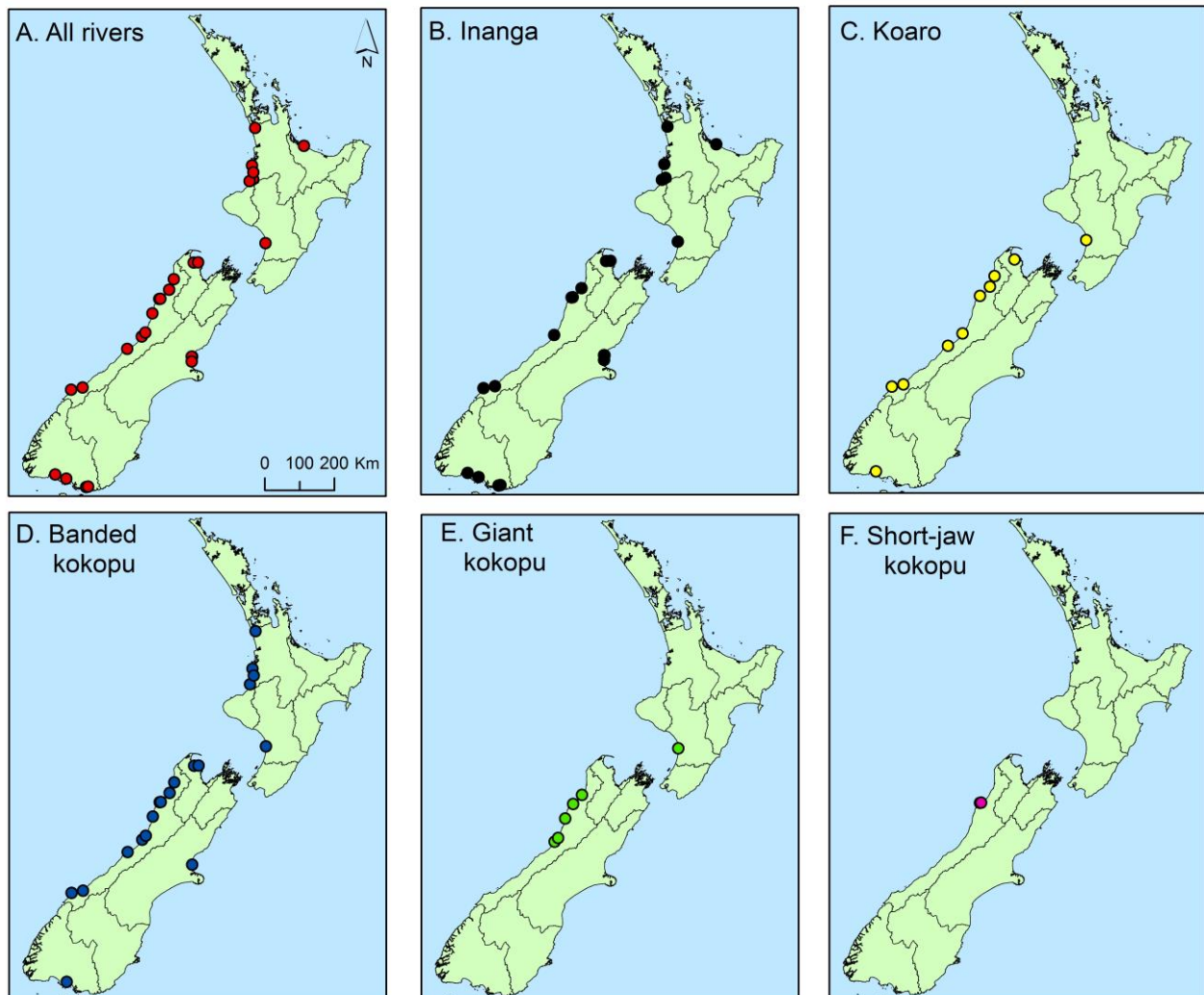
The Buller region has a large number of rivers and is subject to large quantities of rainfall per year (2200 mm) which has been shown to influence coastal productivity (Schiel, 2004). The Westland Current (which has weak mean flows to the north of c. 0.05 ms<sup>-1</sup>) occasionally reverses, causing upwelling of cold waters (Menge *et al.*, 2003). The mean SST is 18.5 °C in summer and 14.1 °C in winter.

### *Westland*

The climate in the Westland region is largely dependent on exposure to weather systems from the Tasman Sea. It is subject to mild conditions with heavy periods of rain. The predominant current is the Westland Current which coupled with southwest winds, creates coastal upwelling of cool nutrient rich waters (Heath, 1972, Chiswell *et al.*, 2015). On average SST

ranges from 17 °C in summer to 13 °C in winter. Chlorophyll-  $\alpha$  levels are elevated in winter reaching a maximum in spring and dropping to lowest levels in summer (Murphy *et al.*, 2001).

From these eight regions, whitebait samples were analyzed from various rivers during a four month period, September to December in 2015 (Fig. 1.4, Table 1.2).



**Figure 1.4.** Map of New Zealand representing rivers where whitebait were collected during the 2015 whitebait season. **a.** All rivers sampled for whitebait. **b.** Samples containing inanga. **c.** Samples containing kōaro. **d.** Samples containing banded kōkopu. **e.** Samples containing giant kōkopu. **f.** Samples containing shortjaw kōkopu.

**Table 1.2** Whitebaiting rivers in New Zealand used for aging and growth studies with species and months sampled.

Region	River	Species	Sep (n)	Oct (n)	Nov (n)	Dec (n)	Region	River	Species	Sep (n)	Oct (n)	Nov (n)	Dec (n)		
Bay of Plenty	Kaituna River	Īnanga	14	15	14		Buller	Mokihinui River	Īnanga	14	18	14			
Waikato	Waikato River	Īnanga	13	14	14				Banded kōkopu	14	15	14			
		Banded kōkopu	15	12					Kōaro	14	8	4			
	Marokopa River	Īnanga	13	14	14				Giant kōkopu				2		
		Banded kōkopu	14	15	2				Orowaiti River	Īnanga	15	2	13		
	Waikawau River	Banded kōkopu	14	13	2	Banded kōkopu				4	3				
	Mokau River	Īnanga	15	15	13					Giant kōkopu				3	
		Banded kōkopu	12	7	2					Shortjaw kōkopu					1
	Awakino River	Īnanga	14	15	14			Karamea River	Banded kōkopu	15	13	15			
Manawatu	Rangitikei River	Īnanga	15	15	14				Kōaro	15	15	14			
		Banded kōkopu	12	12	15				Buller	Īnanga	13	12	15		
		Kōaro	10	12	14					Shortjaw kōkopu				1	
		Giant kōkopu			6			Banded kōkopu				14	16		
	Tasman/ Nelson	Takaka River	Īnanga	9	7	4				Westland	Hokitika River	Īnanga	13	13	15
Kōaro			15	14	7			Banded kōkopu					11	5	
Banded kōkopu			1	16	14	10		Kōaro	11			9	8		
Wainui River		Īnanga	14	15	6		Giant kōkopu						3		
		Banded kōkopu	2	15	14		Cascade River	Īnanga	14		14	15			
Canterbury	Waimakariri River	Īnanga	11	15	15			Banded kōkopu				8	13		
		Banded kōkopu				3		8	Kōaro	8	15	9			
	Saltwater Creek	Īnanga	15	14	14			Waimea Creek	Banded kōkopu			14			
Ashley River	Banded kōkopu			12		Giant kōkopu						12			
Southland	Waiau River	Īnanga	14	14	15		Wanganui River	Banded kōkopu	6	7					
		Kōaro		12				Kōaro	7	7					
	Mataura River	Īnanga	12	14	13		Waiatoto River	Īnanga	11	15	14				
	Aparima River	Īnanga	9	11	11			Banded kōkopu			13	14			
	Titiroa River	Īnanga	13	12	15			Kōaro	15	14	13				
Buller	Punakaiki River	Banded kōkopu		2											
		Giant kōkopu					4								

### **1.2.3 Collection methods**

Whitebait entering rivers and streams form mixed species shoals and are captured by fishers as they migrate upstream (McDowall, 1968, McDowall and Eldon, 1980). Due to the varying behavioural characteristics of each of the whitebait species, such as kōaro which are adept climbers and are often found climbing up the inside of a bucket once caught, these were stirred by hand to mix the species before a subsample of roughly 200 fish was taken (McDowall, 1990).

Whitebait were placed in portable freezers for transportation. Each sample was contained in a ziplock bag with enough water to prevent freezer burn and with waterproof paper stating the location and date written in pencil for future identification along with additional labeling on the bag. Once transported back to the University of Canterbury, the samples were stored at -16 °C.

During previous research (Yungnickel, 2017) samples were defrosted, identified to the species level and measured before transferring each individual fish into small plastic vials containing enough ethanol (70%) to envelop the entire fish. These vials were labeled using pencil on waterproof paper and stored in large ziplock bags that were also labeled for future use. Each sample (plastic bag) of whitebait was then placed into cardboard boxes defined by regions and rivers where they were stored for roughly one year before otolith extraction began in 2017.

### **1.2.4 Otolith extraction**

Once extracted, otoliths can be used to derive an array of statistics about an individual fish such as age, growth and hatch date. This study extracted otoliths from multiple fish from multiple rivers over the course of the settlement period (September-December). By compiling the information gathered from each otolith, valuable insight is provided into the early life history traits of the five whitebait species. Spatial and temporal information will also provide insight into how the five species differs across New Zealand, if any differentiation at all, which will likely aid future management techniques.

## **Chapter 2: Spatial variation in age and growth of īnanga whitebait**

### **2.1 Summary**

- The age of īnanga whitebait was highly variable within and between regions.
- īnanga whitebait entering rivers at lower latitudes were younger than those entering rivers at higher latitudes.
- īnanga whitebait entering rivers at lower latitudes had faster larval growth than those entering rivers at higher latitudes.
- The strength of the positive relationship between age and length for īnanga whitebait varied between regions.
- Hatch dates of īnanga whitebait were predominantly in autumn and coincided with new and full moons.

### **2.2 Introduction**

Species with a wide geographic distribution often encounter a range of environments that exert differing physical and biological pressures on traits. These pressures drive changes in phenotypes or life history traits, causing species to become locally adapted (Bergenius *et al.*, 2005, Barbee *et al.*, 2011). The concept of adaption to local conditions is not new, with empirical evidence frequently cited for terrestrial and freshwater species (De Meester, 1996, Hereford, 2009). Until recently, in contrast marine species were treated as a collection of demographically open populations with large quantities of mixing thought to be occurring between populations. As a result, comparatively fewer studies have been done on how environmental conditions cause local adaptations in marine species (Sanford and Kelly, 2011).

Environmental conditions in marine environments such as sea surface temperature (SST), nutrient levels, pH and other physical parameters display strong spatial variability (Menge *et al.*, 1997, Menge, 2000, Feely *et al.*, 2008). Sea surface temperature has a strong latitudinal gradient, with surface waters generally warmer on average towards the equator and colder towards the poles. For example, average annual SST from 1993-2016 in the subtropics is 17.9 °C, in the Tasman Sea is 15.6 °C and in the Subantarctic is 10 °C (<http://archive.stats.govt.nz>).

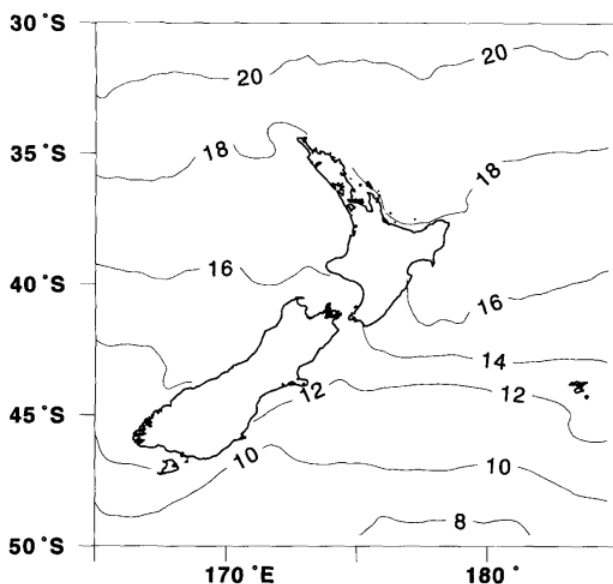


Nutrients underpin the productivity of phytoplankton, which is the base food source for many marine species. Factors such as increased nutrient levels, vertical mixing, light availability and reduced depth of the mixed layer can increase primary productivity. Productivity can be low in the tropics and subtropics due to nutrient limitation and strong thermoclines and pycnoclines (Sigman and Hain, 2012). In general, the highest levels of primary productivity are along the equator (due to divergent upwelling), coastlines, and high latitude oceans such as the Southern Ocean. Coastal waters often have higher levels of productivity due to wind-driven upwelling drawing nutrient rich waters into the euphotic zone (Murphy *et al.*, 2001). Although primary productivity shows large spatial variation across the globe, the strongest variations occur seasonally and is often greatest along the west coasts (Chapter 3, Section 3.2).

Changes in oceanic conditions elicit varying responses in different species, as well as between populations of a single species. For example, Arcto-Norwegian populations of Atlantic cod (*Gadus morhua*) responded to warmer temperatures with increased body length, recruitment and stock size (Nakken, 1994). Conversely, recruitment of cod populations in the North Sea reduced with increasing temperature (O'Brien *et al.*, 2000). Temperature changes have had marked effects on many marine species (Blaxter, 1991, Pepin, 1991, Herbing, 2002). For example, instantaneous daily growth and mortality rates of larval fish increased with increasing water temperature (Houde, 1989). Oxygen uptake has been shown to increase as temperature increases and larval stage duration has been documented to be inversely related to growth rates (Houde, 1989).

The highly variable oceanic conditions around New Zealand are due to its latitudinal spread, isolated location and complex hydrology and topography (Murphy *et al.*, 2001, Ross *et al.*, 2009). Sea surface temperature and primary productivity have received particular attention due to their dominant and widespread effect on marine species. Sea surface temperature around New Zealand displays strong latitudinal variation, with warmer average water temperatures around the North Island than the South. Surface waters at the northern tip of the North Island average 18 °C but reduce with increasing latitude to average 10-11 °C at the southern tip of the South Island (Fig. 2.1). Very little variation is seen between points on the east and west coast at the same latitude (Chiswell, 1994).

Primary productivity around New Zealand is highest along the lower west coast of the South Island and in lower and mid latitudes on the west coast of the South Island (Murphy *et al.*, 2001, Schiel, 2004). Waters in these southern regions have average chlorophyll concentrations that range from 0.1- 1.2 mg m<sup>-3</sup> annually (Murphy *et al.*, 2001). More northerly regions, such as the Bay of Plenty, have average chlorophyll concentrations that on average range from c. 0.1 - 0.4 mg m<sup>-3</sup> annually. Elevated chlorophyll concentrations in southern regions are thought to result from the mixing of warmer subtropical water (macronutrient-poor, but relatively micronutrient-rich) with colder subantarctic water (macronutrient-rich, but micronutrient-poor (Boyd *et al.*, 1999)).



**Figure 2.1.** Average annual sea surface temperature °C from April 1989 to March 1991 for oceanic waters surrounding New Zealand. Source: (Chiswell, 1994).

The wide geographic distribution of īnanga (McDowall, 1968) and New Zealand's variable oceanic conditions suggest that larvae developing in dissimilar coastal water masses will be exposed to differing physical and biological pressures. It is likely that these variable pressures will drive variation in early life history traits such as pelagic growth and age at migration. Most studies of the early life history of whitebait in New Zealand have been completed over small spatial scales (e.g., McDowall *et al.*, 1994, McDowall and Kelly, 1999)), which generally failed to recognise the high spatial variability in oceanic conditions around New Zealand (Barbee *et al.*, 2011).

A large part of what we currently know of whitebait migrations comes from a small number of studies (e.g., McDowall and Eldon, 1980, McDowall, 1984, McDowall, 1990). These studies first postulated that returning whitebait were between 5-6 months old. It was not until

the development of aging techniques such as daily ring counts in otoliths, that the age of migrating fish could be resolved at a fine scale.

Otoliths are the calcareous structures in the inner ear of vertebrates such as teleost fish. They assist in detecting sound and are also used for balance and orientation (Schirripa, 2002, Begg *et al.*, 2005). They are composed of biogenic carbonate, commonly in the form of aragonite, deposited on a protein matrix; these structures sit within a membrane filled with endolymph fluid (Elsdon *et al.*, 2008). In many fish species, otoliths develop daily rings/increments with layers deposited onto their exterior surface daily from fertilisation onwards. This creates a permanent chronology that spans the entire life of a fish (Schmitt, 1984, Elsdon *et al.*, 2008).

By counting daily rings in otoliths, McDowall *et al.* (1994) discovered the age of īnanga whitebait was highly variable. Mean ages from samples ranged from 106 -179 days (d), with overall age ranging from 103-203 d. Although informative, samples collected for McDowall *et al.* (1994) only came from ten rivers. Of these rivers, seven were in the North Island and three were from the South Island, with the large majority located on the east coast of New Zealand. From the information collected in each river, ages were collated to derive the overall age of īnanga.

Although these studies have derived valuable knowledge of early life history traits in the five whitebait species, using this information as the basis for making decisions about local populations may not be appropriate. With differences in oceanic conditions apparent along New Zealand coastlines, and the plasticity and/or local adaptations of some early life history traits, insight into how these early life history traits vary spatially around New Zealand will aid in the development of more realistic population models and future management practices (Barbee *et al.*, 2011).

*The following questions are addressed in this chapter:*

1. *Are there differences between rivers in age at migration of īnanga whitebait?*
2. *Are there regional differences in age at migration of īnanga whitebait?*
3. *Are there regional differences in the hatch date distributions of īnanga whitebait?*

## **2.3 Materials and methods**

### **2.3.1 Sample selection**

In total, 793 post-larval īnanga were collected on 48 dates between the 1 September and 30 November 2015. The subset of samples used for this Chapter is shown in Table 1.2. From the subset of samples, up to 15 whitebait were used from each river/month for otolith extraction. Sample sizes varied due to method constraints such as pigmentation of fish (see below) or because of failure (usually cracking) of otoliths during the preparation/polishing process.



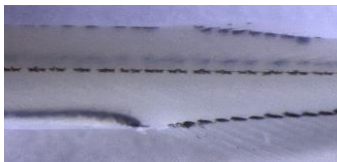

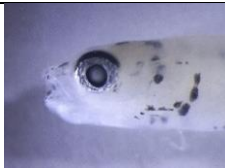
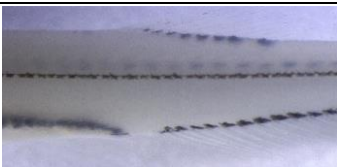
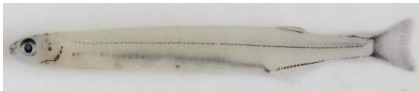

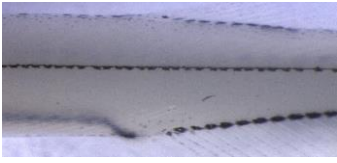
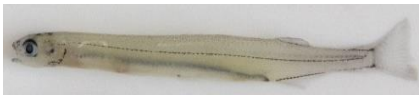

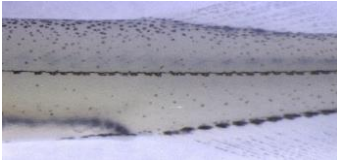


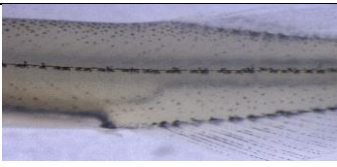


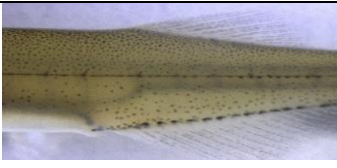
### **2.3.2 Fish selection**

To keep extractions structured and orderly, only samples from one river per month were processed at any given time. From each river sample, 15 vials (each containing one fish) were removed from the storage bag and set aside for dissection with only one fish dissection being done at a time to maintain individual identification. The fish was placed into a plastic petri dish under a stereo microscope and checked for development of pigmentation ('speckling').

When whitebait first enter freshwater they are transparent, with some showing dominant xanthophores and melanophores. The xanthophores are present as two mid-dorsal rows along the trunk of the body and in speckling across the head region. Melanophores show strong pigmentation along the lateral line of the fish and are usually scattered along the ventral side of the fish and surrounding the eyes and mouth (McDowall, 1968). Every fish shows variation in coloration and placement of the pigments, but they are very distinct and not easily confused with pigmentation that develops after entry into freshwater (Table. 2.1).

Pigmentation begins to intensify shortly after whitebait enter freshwater (McDowall, 1968). The pigmentation can be described as 'speckling' over the trunk of the fish, usually beginning dorsally and developing ventrally towards the mid-lateral line. As the individual remains in freshwater, the 'speckling' intensifies to form a mottled pattern over the body. A silver guanine layer begins to form in the lining of the abdominal cavity and on the inner surface of the latero-ventral operculum (Woods, 1968). Because the body wall of whitebait is translucent, the guanine layer (when present) is visible to the naked eye (McDowall, 1968, Woods, 1968). Any whitebait that displayed 'speckling' were not used for this study and were placed back into their vial. This was to ensure only fish that had very recently entered the river ('fresh run') were used.

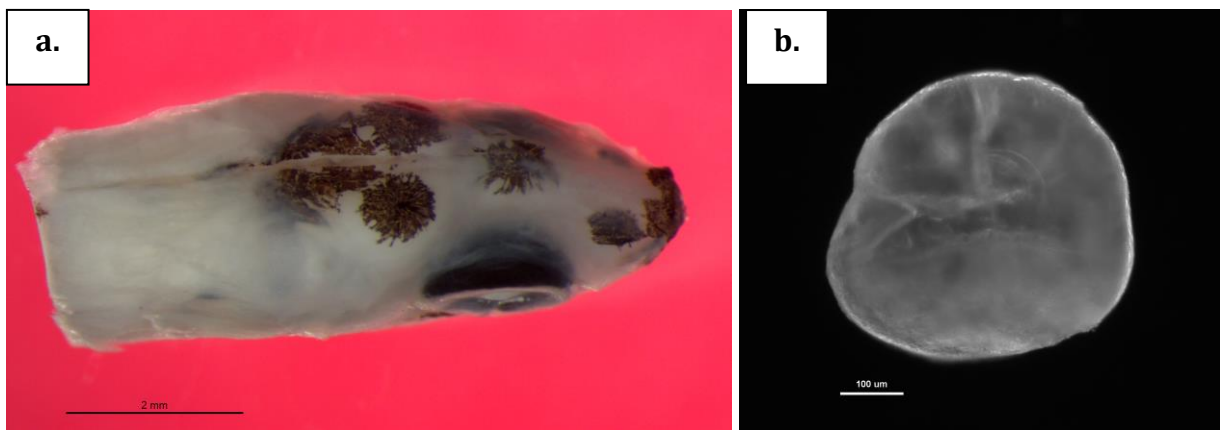
**Table 2.1.** The six stages of pigmentation development that occur once whitebait enter freshwater. Pictures are of īnanga (*G. maculatus*) whitebait. Source: (Yungnickel, 2017).

Stage	Stage of development	Description	Photos		
			Whole Fish	Head	Anal and Dorsal offset
1	Clear fish	Clear with some mottled melanophores characteristic of each species.			
2	Lightly pigmented	Development of a few fine melanophores along the dorsal surface of the fish.			
3	Pigmented	Development of strong speckling mainly along the dorsal surface of the fish.			
4	Highly pigmented	Development of strong melanophores all over the fish and often some internal organs. V-shaped lines of melanophores develop along the myotomes.			
5	Silver abdomen	Development of a silver belly			
6	Juvenile fish	Development of strong colour and a full silver belly			

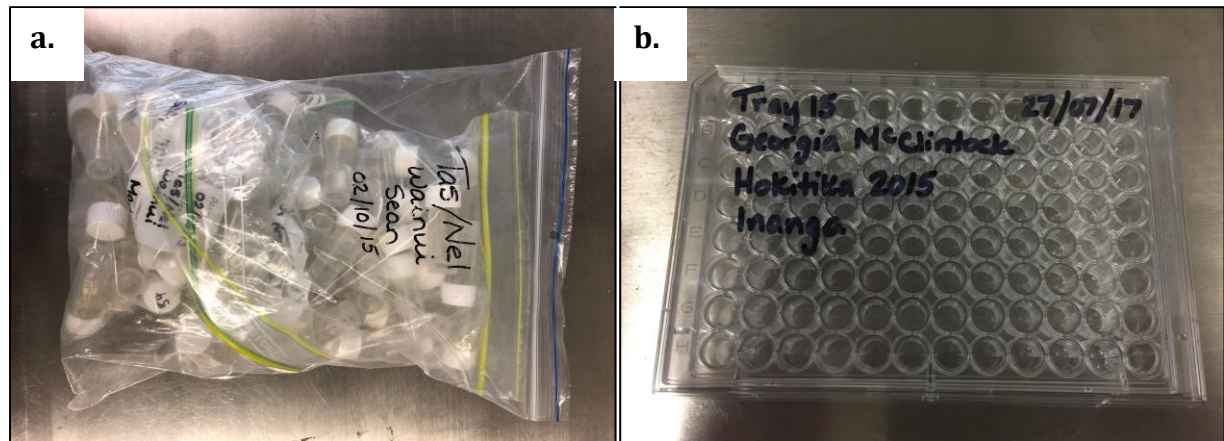
### 2.3.3 Dissection

All dissections took place using a stereo microscope. Dissection began by separating the head from the body using a scalpel and cutting directly anterior to the pectoral fins. An incision was made dorsally along the longitudinal axis of the cranium to expose brain matter, which was removed using extra fine tipped forceps to allow easy location of the sagittal otoliths (Fig. 2.2.a). Both sagittae were removed with forceps, taking particular care not to crush them. Sagittae were cleaned using distilled water and a soft, fine-tip paintbrush, gently brushing over the otoliths until all excess organic material was removed (Fig. 2.2.b).

Each cleaned sagitta was transferred into a well in a microplate that contained 96 numbered wells. The left sagitta was placed into the first available well and the right sagitta into the adjacent well. Transfer involved wetting the tip of the paintbrush and running it gently over a sagitta. Once the sagitta had adhered to the paintbrush it could be placed into the well by brushing it against the bottom or inner sides of the well. To keep a record of where individual sagittae were stored, each tray was assigned a number and labeled with region/river/month collected. The location of each sagitta was recorded on an Excel spreadsheet (Appendix 1).



**Figure 2.2.** **a.** Head of an īnanga whitebait (*G. maculatus*) using a light microscope (6x magnification) that has been separated from the body and with a longitudinal incision made along the cranium. **b.** Photomicrograph of an extracted and cleaned īnanga whitebait otolith under a compound microscope.



**Figure 2.3.** a. Plastic bags used for storing whitebait samples until dissection, all bags were labeled and stored in boxes corresponding to region and b. Microplate containing 96 wells used for storing sagittae, each plate was numbered and labeled by region.

### 2.3.4 Sagitta mounting and polishing

Only the left sagitta was initially prepared for polishing. The right sagitta was stored and used if the left sagitta was broken or over-polished during the subsequent aging procedure. The left sagitta was set on a glass slide, sulcus-side-up, using Crystalbond™ 509 adhesive. A small fragment of Crystalbond was placed in the center of the glass slide which was transferred to a hot plate that was pre-heated to 195 °C. Once the Crystalbond was softened (c. 10 s) the slide was removed and placed onto a stereo microscope stage while the Crystalbond cooled and hardened. Using a fine-tip paintbrush, the sagitta was transferred onto the top of the Crystalbond mound, sulcus-side-up. The slide was then placed back onto the hot plate to re-soften the Crystalbond and then returned onto the microscope stage. Using 16x magnification, the otolith was quickly and firmly pressed into the Crystalbond, ensuring it remained level and was completely covered by the setting medium while taking care not to introduce air bubbles. Individual identification was maintained by etching the unique fish number of the fish onto the glass slide.

Once mounted, sagittae were hand-polished using South Bay Technology aluminium oxide 12 µm and 0.3 µm lapping film to remove excess Crystalbond and to visualise growth rings. Using wet (nanopure) lapping film, the otolith was gently polished using a circular motion. The slide was rinsed in a beaker of nanopure water and dabbed dry using a Kimwipe®. The extent of polishing of the sagitta/crystal bond was checked with a Zeiss AxioImager.M1 compound microscope, equipped with Differential Interference Contrast (DIC) illumination and using 20x and 40x EC Plan-NEOFLUAR objectives. This procedure of sanding /



washing / viewing was repeated until there was a clear view of growth rings from the core to the post-rostral edge. If necessary, the sagitta was flipped and re-set, sulcus-side-down, to achieve better visibility of the growth rings. The 0.3 µm lapping film was used in a finishing procedure to remove any coarse polishing marks.

### **2.3.5 Setting**

Before photomicrographs were captured, polished sagittae were soaked in immersion oil (Zeiss Immersol 518N) for 24 hours by placing a drop of oil directly over the polished otolith. The sagitta was then covered with a glass cover slip (avoiding air bubbles) that was set in place with a drop of clear nail varnish (Revlon Colourstay TOP COAT) at each corner.

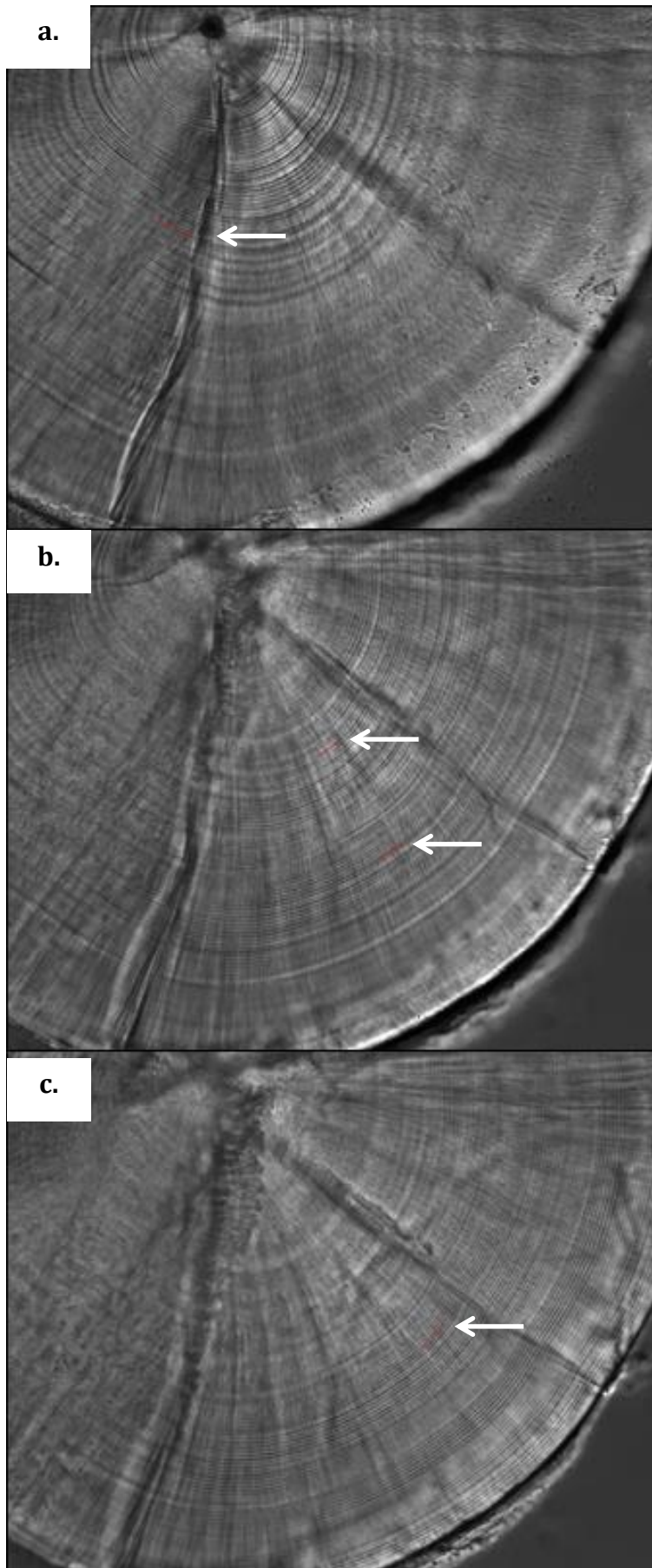
### **2.3.6 Photomicrographs**

Sagitta samples used for aging were viewed with a Zeiss AxioImager.M1 compound microscope, equipped with Differential Interference Contrast (DIC) illumination and using 20x and 40x EC Plan-NEOFLUAR objectives. Photomicrographs were captured using a Zeiss AxioCam 506 monochrome camera with Zeiss ZEN 2.3 Pro (Blue Edition) software. All photomicrographs were captured using the 40x objective lens. The hatch-mark was located near the core of the sagitta and used as the starting point for aging. The hatch-mark is an obvious, well-defined ring distal to the core (McDowall *et al.*, 1994). Many sagittae required image capturing at different focal planes to view a continuous sequence of daily rings from the core to the post-rostral edge. To accurately keep track of in-focus daily rings, red annotation points were added to the images (Fig. 2.4).

### **2.3.7 Aging**

Photomicrographs were imported into Image-Pro Premier v. 9.1 software. Using the Otolith Application within the Image-Pro software, daily rings were counted from the hatch mark to the post-rostral edge. Estimates of age were obtained from the total count of rings and growth was defined by daily increment widths. Each increment found by the software was re-checked manually and sub-daily rings were excluded. The total number of daily rings and the increment distance between daily rings was recorded and imported to Excel for further analysis.





**Figure 2.4.** The process of photographing an īnanga whitebait (*G. maculatus*) sagitta using a Zeiss AxioImager.M1 compound microscope, equipped with Differential Interference Contrast (DIC) illumination and using 40x objective. The three panels show a series of photomicrographs of the same otolith with red annotation lines (highlighted by white arrows) that are used as a reference point during the later computational aging process.

## **2.4 Data analysis**

### **2.4.1 Spatial variation in age and growth rate**

#### *Age*

The number of daily rings between the hatch mark and post-rostral margin at the time of capture was used as a proxy for age, where one ring was equal to one day (Campana, 2001, McDowall *et al.*, 1994). Welch two-sample t-tests were used to compare rivers, but for comparisons between more than two rivers, one-way ANOVAs were used. Post hoc comparisons were completed using Tukey HSD tests. Īnanga collected during September 2015 were used for spatial age comparisons.

#### *Growth*

Average daily pelagic growth rate for each whitebait was calculated by measuring the increment width ( $\mu\text{m}$ ) between each deposited daily ring and then taking the average across all increments. Welch two-sample t-tests were used to compare rivers, but for comparisons between more than two rivers, one-way ANOVAs were used. Post hoc comparisons were completed using Tukey HSD tests. Īnanga collected during September 2015 were used for spatial growth comparisons.

## 2.5 Results

### 2.5.1 Age at migration - variation within regions

#### *Waikato*

The age (days) of īnanga whitebait entering the four rivers in the Waikato region varied significantly between rivers ( $F_{3,51} = 7.503$ ,  $p < 0.05$ , Fig. 2.5). Post hoc comparisons (Tukey HSD,  $p < 0.05$ ) determined īnanga entering the Marokopa River ( $\bar{x} \pm \text{SE age: } 167.3 \pm 5.7 \text{ d}$ ) were older than those entering the Awakino River ( $142.4 \pm 3.2 \text{ d}$ ) and the Waikato River ( $145.4 \pm 3.7 \text{ d}$ ). Īnanga entering the Mokau River ( $160.4 \pm 4.4 \text{ d}$ ) were older than those entering the Awakino, but were not significantly different from any of the remaining rivers.

#### *Tasman/Nelson*

Īnanga whitebait entering the Takaka and Wainui Rivers were very similar in age ( $t = 0.05$ ,  $p = 0.65$ , Fig. 2.5). However, only a small sample ( $n=9$ ) of whitebait could be obtained from the Takaka River in September.

#### *Canterbury*

The age of īnanga whitebait entering the two rivers within the Canterbury region varied significantly in September 2015 ( $t = -3.40$ ,  $p < 0.05$ , Fig. 2.5). Īnanga whitebait entering the Waimakariri ( $\bar{x} \pm \text{SE age: } 168.2 \pm 3.4$ ) were younger than those entering Saltwater Creek ( $184.2 \pm 3.3$ ).

#### *Southland*

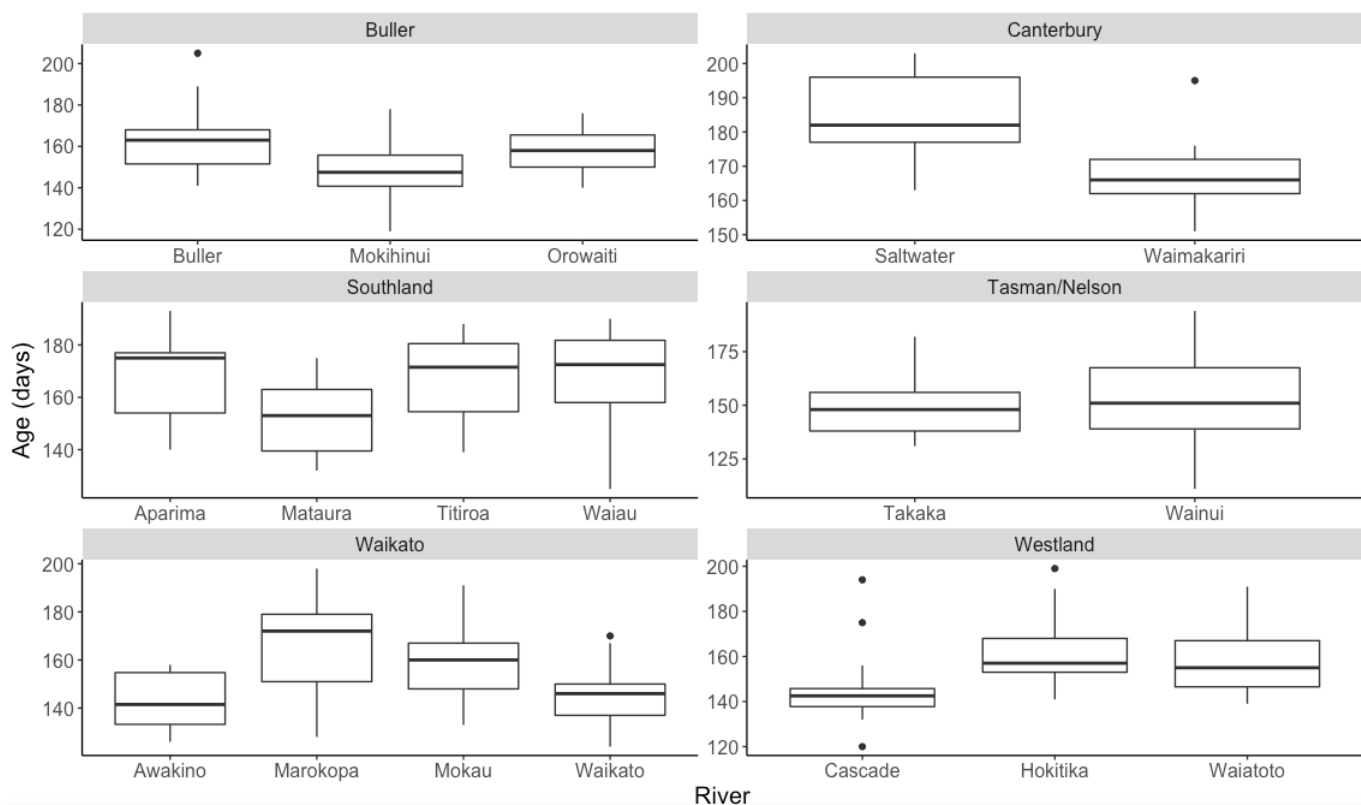
From the rivers sampled within the Southland region, the average age of post-larval īnanga entering the Maitai, Waiau, Aparima and Titiroa Rivers did not differ significantly ( $F_{3,45} = 2.493$ ,  $p = 0.07$ , Fig. 2.5). Average ages of fish entering rivers within the Southland region showed little variation ranging from 152.5 to 169 d.

#### *Buller*

In September 2015, the age at migration of īnanga whitebait entering rivers in Buller varied significantly between rivers ( $F_{2,41} = 3.916$ ,  $p < 0.05$ ; Fig. 2.5). This was due to whitebait entering the Mokihinui ( $\bar{x} \pm \text{SE age: } 147.8 \pm 4.4 \text{ d}$ ) being significantly younger (Tukey HSD,  $p < 0.05$ ) than those entering the Buller ( $163.3 \pm 4.7$ ). There was no significant difference between the age at migration of whitebait entering the Orowaiti and either of the other rivers.

### Westland

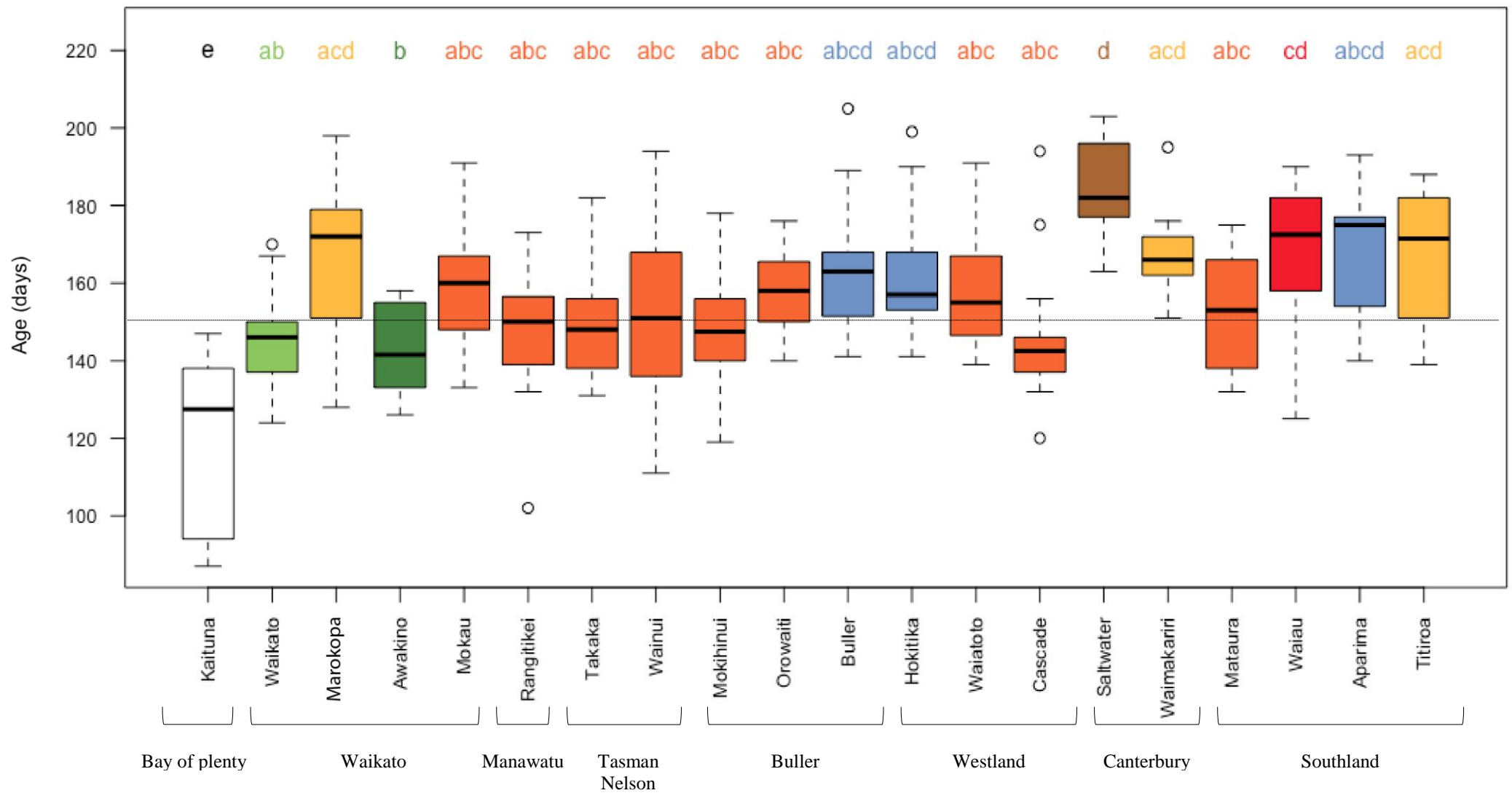
The average age of post-larval īnanga entering rivers in the Westland region was relatively consistent (146.3 to 162.2 d) and did not vary significantly between rivers ( $F_{2,35}=3.083$ ,  $p = 0.06$ , Fig. 2.5).



**Figure 2.5.** Age at migration (days) for īnanga whitebait (*G. maculatus*) between multiple rivers in New Zealand, categorized into regions. Samples were collected in September 2015. Boxplots show maximum age, upper quartile, median, lower quartile and minimum age.

### **2.5.2 Age at migration - variation between rivers**

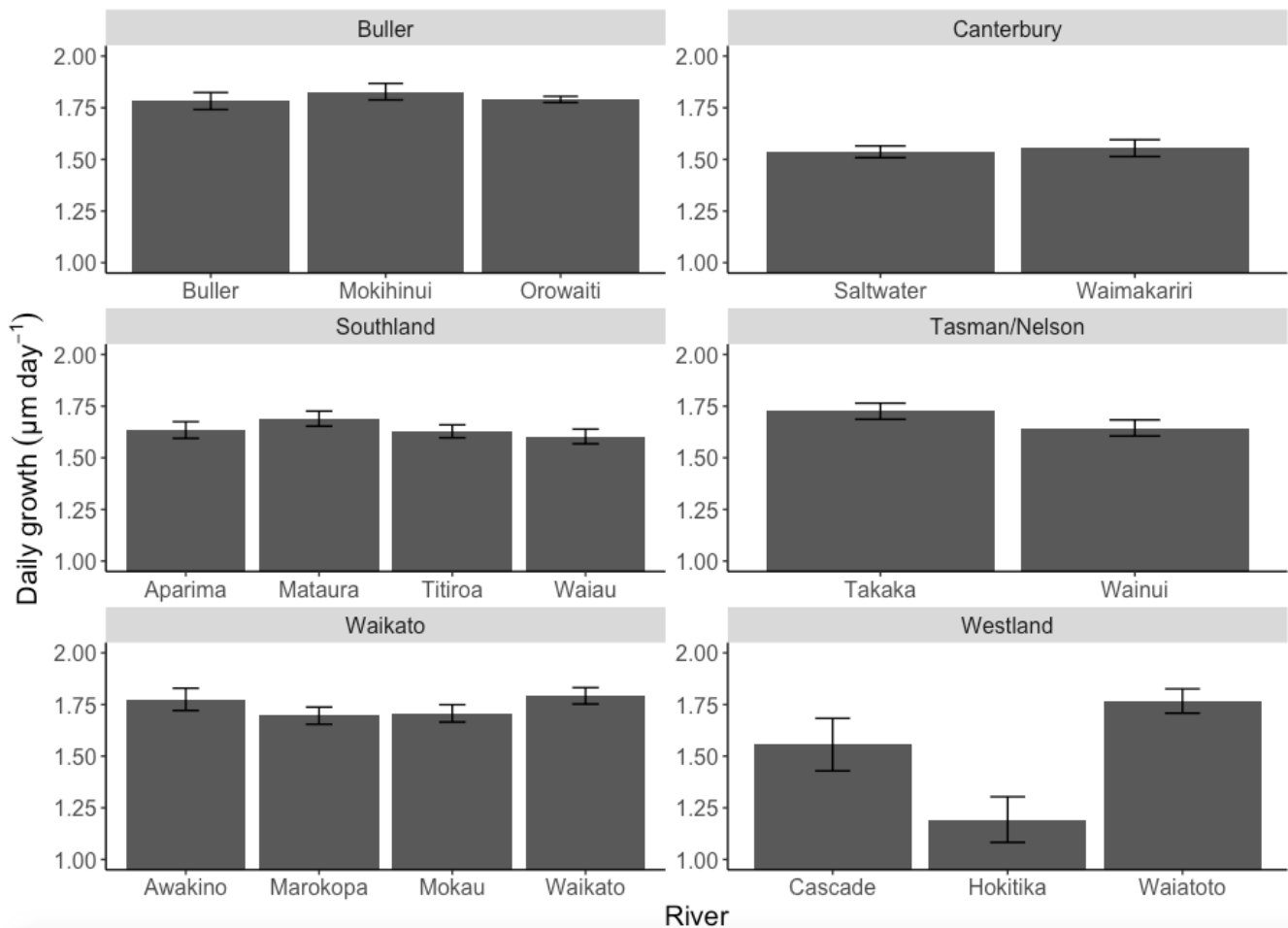
The mean age at migration of īnanga whitebait entering all rivers was compared. In September 2015, the age at migration of īnanga whitebait entering rivers across New Zealand differed significantly ( $F_{19,244}=9.216$ ,  $p<0.05$ ). Post hoc comparisons (Tukey HSD,  $p<0.05$ ) showed significant differences between multiple rivers (Fig. 2.6). Īnanga whitebait entering the Kaituna River (Bay of Plenty;  $\bar{x} \pm \text{SE}$  age:  $118.2 \pm 6.1$  d) were significantly younger than those entering any other river. On average, whitebait in the Kaituna River were 24 d younger (20.4%) than those in the river with the next youngest fish, the Awakino (Waikato;  $142.4 \pm 3.2$  d). Some of the oldest īnanga whitebait were sampled from Canterbury rivers: Waimakariri River ( $\bar{x} \pm \text{SE}$  age:  $168.18 \pm 3.4$  d) and Saltwater Creek ( $184.20 \pm 3.3$  d).



**Figure 2.6.** Age at migration (days) of īnanga (*G. maculatus*) whitebait entering 20 New Zealand rivers during September 2015. Boxplots show the maximum, upper quartile, median, lower quartile and minimum age. Colours and letters above rivers are results of post hoc comparisons (Tukey HSD,  $P < 0.05$ ). Rivers that share letters or colours do not differ significantly. Dotted line denote overall mean.

### 2.5.3 Daily pelagic growth rate - within region variation

Overall, average daily growth rates within each region showed little variation. For September 2015, only the Westland region ( $F_{2,35} = 6.864$ ,  $P < 0.05$ , Fig. 2.7) had significant variation in growth rates between rivers. The average daily growth rate of īnanga whitebait entering the Hokitika River ( $\pm$  SE:  $1.19 \mu\text{m d}^{-1} \pm 0.11$ ) was significantly lower than that of fish entering the Cascade ( $1.56 \mu\text{m d}^{-1} \pm 0.13$ ) and Waikatoto River ( $1.77 \mu\text{m d}^{-1} \pm 0.06$ ).

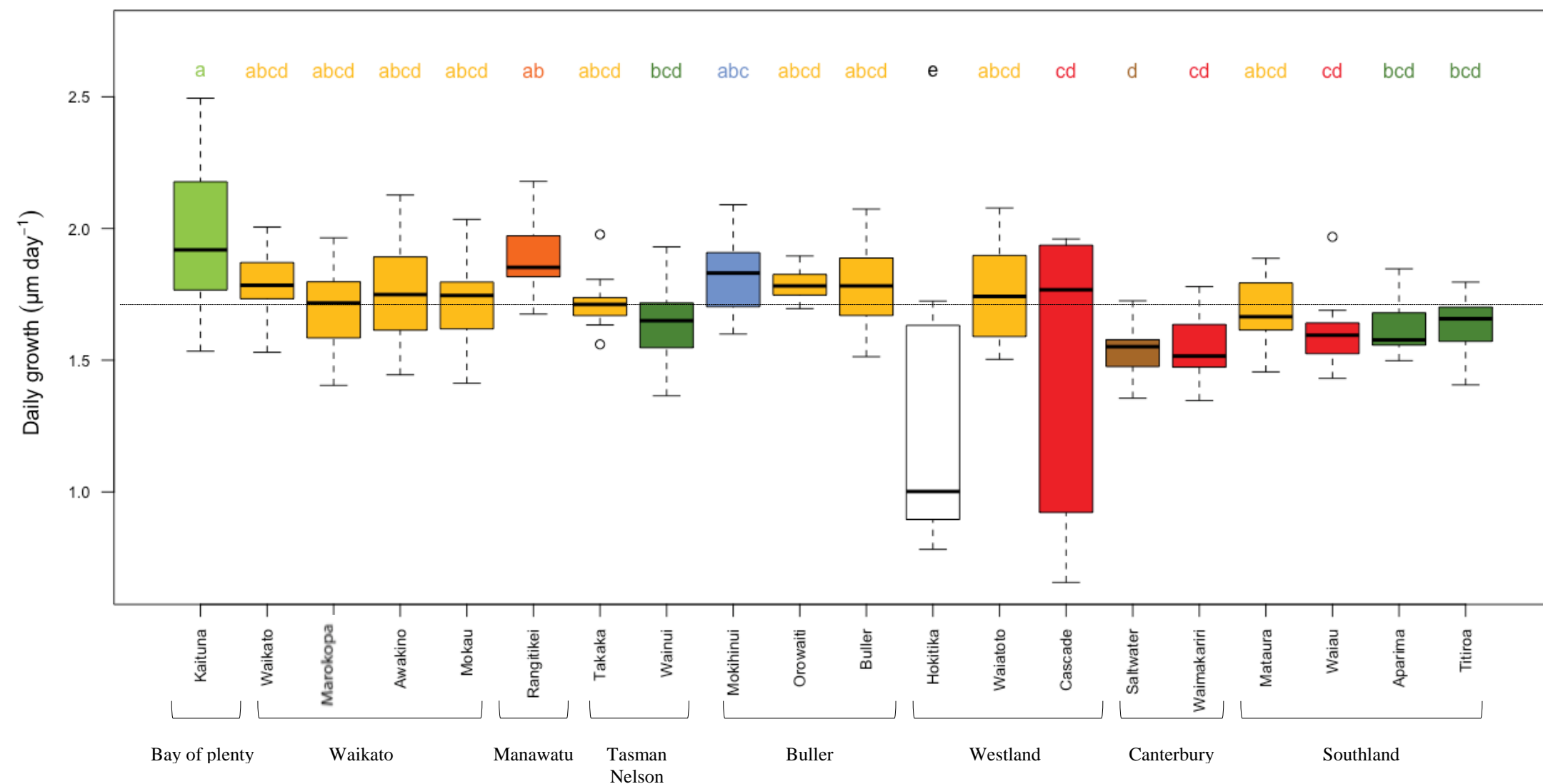


**Figure 2.7.** Mean ( $\pm$ SE) daily pelagic growth rate of inanga whitebait (*G. maculatus*) entering 18 rivers in six regions during September 2015.

#### **2.4.4 Daily pelagic growth rate - between river variation**

There was large spatial variations in daily pelagic otolith growth across all 20 rivers ( $F_{19,244} = 8.626$ ,  $P < 0.05$ , Fig. 2.8). Overall, the Kaituna River (Bay of Plenty) had the highest daily growth ( $1.96 \mu\text{m d}^{-1}$ ) with a slow decline in growth rates with increasing latitude. The Hokitika River had the lowest average daily otolith growth rate ( $1.19 \mu\text{m d}^{-1}$ ). Rivers at the same latitudes but on differing coasts did display some differences in daily pelagic growth. For example, īnanga whitebait entering the Waimakariri River ( $1.55 \mu\text{m d}^{-1}$ ) and Saltwater Creek ( $1.54 \mu\text{m d}^{-1}$ ) on the east coast displayed lower levels of growth than whitebait entering the Waikatoto River ( $1.77 \mu\text{m d}^{-1}$ ) which is at similar latitudes on the West Coast.





**Figure 2.8.** Daily pelagic growth rate ( $\mu\text{m d}^{-1}$ ) of īnanga (*G. maculatus*) whitebait entering 20 New Zealand rivers during September 2015. Boxplots show the maximum, upper quartile, median, lower quartile and minimum age. Colours and letters above rivers are results of post hoc comparisons (Tukey HSD,  $P < 0.05$ ). Rivers that share letters or colours do not differ significantly. Dotted line denotes overall mean.

## 2.6 Discussion

The age of īnanga whitebait entering rivers of New Zealand have high levels of variation within each river and within regions across New Zealand. Overall, the age of īnanga whitebait was found to range from 76 d to 226 d, which is consistent with studies such as McDowall *et al.* (1994) that found ages ranging from 103 d to 203 d. From comparisons among rivers within regions of New Zealand, four of the six sampled regions exhibited significant differences in age. This within-region variability suggests there are some levels of separation between rivers within a region.

With the growing recognition that marine species are not a collection of demographically open populations that express high levels of gene flow (Levin, 2006). The idea of differentiation or distinction occurring in widespread species such as whitebait is not unusual (McDowall, 1968). Population differentiation has previously been recorded in marine species with a planktonic stage and arises due to restricted connectivity between populations (Sotka *et al.*, 2004). This restricted connectivity is usually due to life history, larval behaviour and/or oceanographic features that lead to the retention of larvae near their natal habitat, followed by local adaptation to local environments. Possible connectivity restrictions surrounding New Zealand's coastlines could arise from its large latitudinal spread, complex bathymetry and topography and ocean currents (Murphy *et al.*, 2001). For example, whitebait originating from the Bay of Plenty region will not likely reach other regions such as the Southland because of coastal currents (Fig. 1.3).

Within regions there is no apparent trend in what is driving differentiation between populations. It is only when comparisons are made at a New Zealand-wide scale (all rivers compared) that a strong latitudinal gradient becomes apparent. Fish entering rivers in the lower latitudes of New Zealand (North Island) are younger and with the progression south to higher latitudes fish tend to be on average older (South Island).

This spatial variability in age that is seen in the study has also been documented in an Australian study conducted by Barbee *et al.* (2011). Results from that study concluded age at migration of īnanga tended to be younger for individuals entering Australia rivers than for those in New Zealand rivers (Rowe and Kelly, 2009). Drivers of this variation were attributed to differences in water temperature, food availability and larval mortality owing to starving or

predation (Houde, 1989, Leggett and Deblois, 1994, Searcy and Sponaugle, 2001). Warmer sea temperatures are known to promote faster turnover times in larval populations with increased levels of growth and reduced pelagic larval durations seen in populations. In colder, more temperate seas, longer turnover times are seen as a result of slower growth and longer pelagic larval durations (Houde, 1989, Green and Fisher, 2004).

Water temperatures display a long latitudinal gradient. Water temperatures around the North Island are on average warmer than temperatures around the South Island (Chiswell, 1994). Average temperatures range from 18 °C off the northern tip of the North Island to 10 °C off the southern tip of the South Island. From my study it can be suggested that warmer sea temperatures experienced at lower latitudes drive the shorter pelagic larval durations (age at migration) of whitebait entering northern rivers such as the Kaituna (Bay of Plenty). Conversely, lower sea temperatures at higher latitudes may drive the longer pelagic larval durations of whitebait entering southern rivers such as Mātaura (Southland).

The latitudinal variation in age of īnanga whitebait showed some differentiation between the east and west coasts of New Zealand. Whitebait entering rivers in the Canterbury region (East Coast) such as Saltwater Creek and Waimakariri River were on average 184.2 and 168.2 d old. Whitebait entering rivers in the Westland region (West Coast) at similar latitudes, such as Hokitika River, were considerably younger at 162.2 d. The environmental condition likely responsible for this differentiation is primary production. Increased levels of primary production have been shown to increase growth rates and decrease pelagic larval durations (Searcy and Sponaugle, 2001). Primary production at the mid region of the west coast of the South Island and the upper northeast coast of the North Island are on average higher than the east coast of the South Island due to wind-driven upwelling (Schiel, 2004). This variation in primary productivity has also been linked to morphological variation (total length) in īnanga whitebait. Higher levels of primary production on the west coast of the South Island were suggested to be responsible for the greater size of īnanga whitebait in this region (Yungnickel, 2017).

It seems likely that oceanic conditions affecting age at migration are also affecting the variability seen in growth. However, average daily pelagic growth rates of īnanga ( $\mu\text{m d}^{-1}$ ) showed very little variation between rivers of New Zealand. Comparisons of growth within

regions revealed significant differences in only one region (Westland). In Westland, the findings were driven by the extremely low growth rates documented in the Hokitika River ( $m = 1.19 \mu\text{m d}^{-1}$ ).

As with the age at migration of īnanga whitebait, it was only when individual rivers were compared that a latitudinal trend in growth rates became apparent. Conversely to age, growth rate is highest in the lower latitudes of New Zealand and lower in the higher latitudes. These results suggest īnanga whitebait in the lower latitudes of New Zealand have dissimilar early life history traits to those in the lower portions of the South Island. Īnanga whitebait at lower latitudes have “get in, get out” early life history with a short pelagic larval duration because of faster daily growth rates. Īnanga whitebait in these areas have also been shown to exhibit smaller body sizes at migration (Yungnickel, 2017). Whitebait at higher latitudes remain in the pelagic environment for longer, have on average slower daily growth rates and are larger when they enter freshwater (Yungnickel, 2017).

## **Chapter 3: Temporal variation in the age and growth of īnanga whitebait**

### **3.1 Summary**

- Overall, post-larval īnanga migrating at the end of the settlement period (September-November) were younger than those migrating earlier.
- Age at migration did not follow the same trend within regions at the river level.
- Overall, the daily pelagic growth rate of īnanga whitebait appeared to increase towards the end of the settlement period, but this was not statistically significantly.
- Daily growth rates were highest in post-larval īnanga entering North Island rivers with most exhibiting an increase in growth towards the end of the settlement period.
- Age – length relationships showed a weak, positive, correlation that varied between rivers and months.

### **3.2 Introduction**

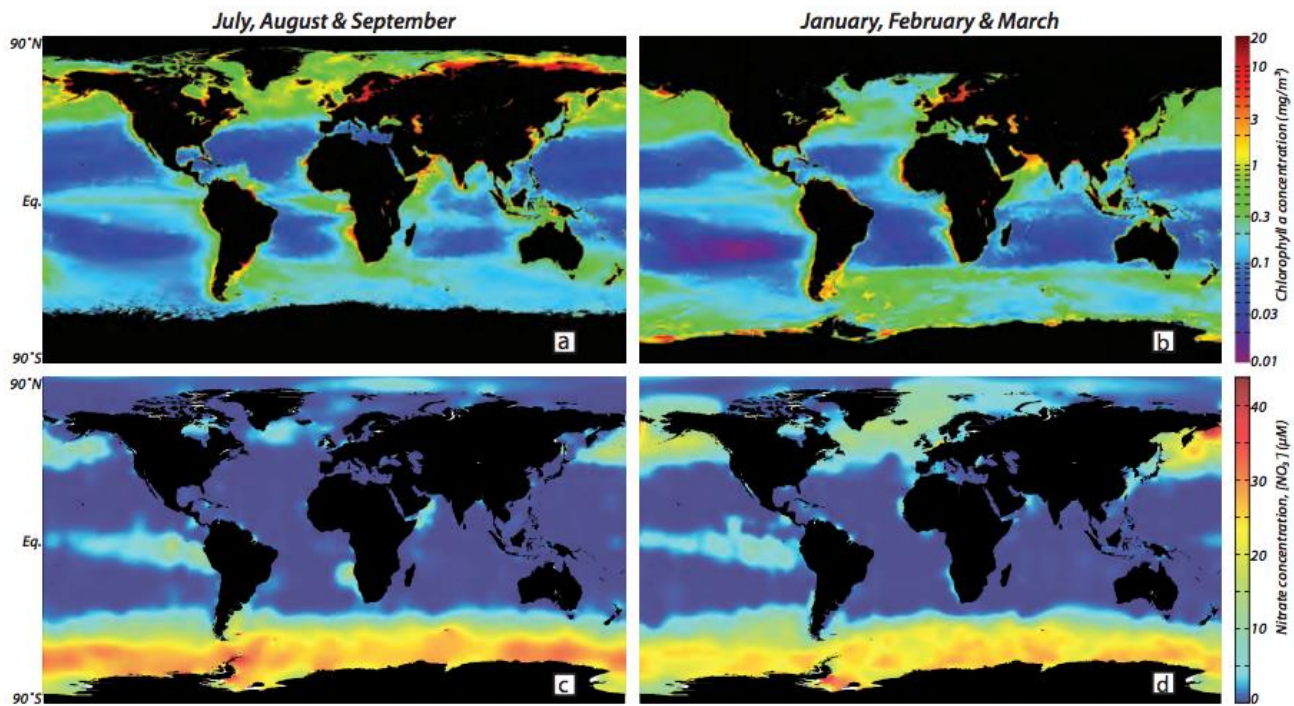
The ocean is a highly heterogeneous ecosystem with strong spatial variation in oceanic conditions at global and local scales (see Chapter 1, Section 2.1). Furthermore, temporal variation in oceanic conditions results from direct or indirect responses to time-based external atmospheric forcing (Stammer and Wunsch, 1999). Strong temporal fluctuations are readily seen in sea surface temperature (SST), productivity and salinity (Mitchell and Wallace, 1992, Rao and Sivakumar, 2003, Sigman and Hain, 2012).

Strong annual fluctuations in SST are caused by the tilt of the earth's axis as it rotates around the sun. Maximum SST is recorded in August/ September in the Northern Hemisphere and minimum SST is recorded in February/March. The opposite occurs in the Southern Hemisphere where maximum SST's are recorded in February/March (Mitchell and Wallace, 1992). The extent of annual fluctuations in SST depends largely on the region (e.g., areas along the equator and those with the highest SST averages have the lowest annual fluctuations). In the western equatorial Pacific Ocean, the amplitude of SST annual fluctuations is as low as 0.5°C in some areas (Wyrтки, 1965). Towards higher latitudes the amplitude of annual variation increases, with some temperate regions having SST amplitudes of up to 8°C (Wyrтки, 1965).

Salinity levels in the ocean are governed by changes in rainfall, runoff, wind, melting glaciers, circulation of water masses and evaporation (Rao and Sivakumar, 2003). After temperature, salinity is the next most important oceanic physical property that controls thermodynamic behaviour, vertical mixing, depth of penetrative convection and thermohaline circulation. Sea surface salinity (SSS) shows strong seasonal variation across the globe with variations being most pronounced in the tropics and the North Indian Ocean (Levitus, 1986, Hénin, Du Penhoat and Ioualalen, 1998).

Ocean productivity also exhibits strong seasonal fluctuations (Chapter 2, Section 2.1). Physical processes in the ocean such as circulation, mixed layer dynamics, upwelling, nutrient cycling, deposition of atmospheric dust and the solar cycle are known to be growth-limiting factors for phytoplankton and therefore productivity (Behrenfeld *et al.*, 2005, Sigman and Hain, 2012). Productivity in the ocean is often greatest in summer/spring when more light is available and when reduced wind driven turbulence (mixed layer depth) prevents phytoplankton being mixed into deeper and darker water (Fig. 3.1). The onset of spring is also associated with warming and freshening of water, increasing the buoyancy of surface waters that often leads to large mixed layer shoals of phytoplankton known as ‘spring blooms’ (Sigman and Hain, 2012). Seasonal variation in productivity is greater towards higher latitudes (e.g., spring blooms in the North Atlantic extend over scales of more than 2000 km (Siegel, Doney and Yoder, 2002).

Similar to spatial changes in oceanic conditions, temporal changes are also found to influence marine species (Skjoldal, Gjøsæter and Loeng, 1992). Temporal changes in oceanic conditions have been shown to directly and indirectly affect growth rates, developmental time, swimming performance, and mortality rates of larval fish (Gallego *et al.*, 1996, Arendt, 1997, Meekan *et al.*, 2003). For example, Meekan *et al.* (2003) found SST recorded during warmer summers explained more variation in the growth of larval neon damselfish (*Pomacentrus coelestis*) than chlorophyll and zooplankton concentrations. Planktonic composition has also been shown to express large transformations in response to variability in climatic conditions. Hooff and Peterson (2006) found zooplankton composition reflected seasonal changes in oceanic conditions along the Oregon coast.



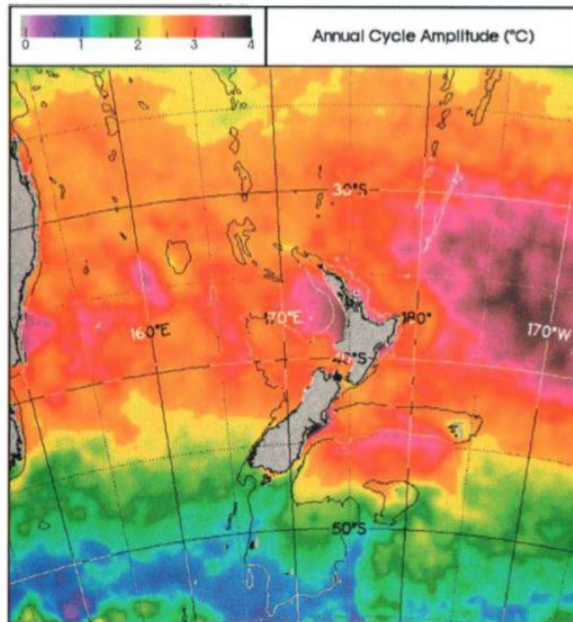
**Figure 3.1.** Global map of ocean concentrations of satellite-derived chlorophyll and ship sampled nitrate ( $\text{NO}_3^-$ ; the dominant N-containing nutrient). The Northern hemisphere summer is shown in the left panels and the Southern hemisphere summer on the right. Source: (Sigman and Hain, 2012).

Winter upwelling drew subtropical neritic fauna (high in diversity, but low in biomass) to the coast. In comparison, summer upwelling drew water from the north that brought in copepod communities of sub-arctic boreal species that were high in biomass but low in diversity.

Temporal changes in oceanic conditions are a prominent feature of New Zealand's coastal waters. Hot and dry summers are followed by cool and wet winters. Sea surface temperature shows prominent interannual variability, with maximum temperatures being reached in February and minimum temperatures around August (Chiswell, 1994). The amplitude of seasonal fluctuations in SST exhibits a relationship with patterns in oceanographic circulation. For instance, the East Auckland, East Cape and Antarctic Circumpolar Currents all have small annual cycles with temperature amplitudes of 2.5-3.5°C (Fig. 3.2). Sub-Antarctic waters vary by less than 1°C in temperature whereas nearshore neritic waters may vary by more than 4°C (Uddstrom and Oien, 1999).

Ocean productivity (chlorophyll levels) in New Zealand's coastal waters is highest in spring and autumn and lowest in winter with an annual variation of c. 0.1  $\text{mgm}^{-3}$  (Murphy *et al.*, 2001). To the east of the North Island, chlorophyll levels are elevated during winter and reach a maximum in spring before falling to a minimum towards the end of summer. Subtropical

regions, such as Bay of Plenty, Waikato and Manawatu, show very little seasonal variation in chlorophyll but reach a maximum in spring. Sub-Antarctic waters show a weak, but detectable, annual cycle with minimum productivity in late winter and maximum in late summer/early autumn (Murphy *et al.*, 2001).



**Figure 3.2.** Sea surface temperature annual cycle amplitude (°C) surrounding New Zealand. Source: (Uddstrom and Oien, 1999).

Understanding how temporal changes in oceanic conditions influence larval traits such as growth and age at migration will prevent incorrect generalisations about widely dispersed species. With this in mind, research on the whitebait fishery and its five constituent species has begun to incorporate temporal aspects. Most of the basic biology of these species has come from extensive research by a few researchers (e.g., McDowall, 1964, Benzie, 1968, McDowall and Eldon, 1980). Predominantly, temporal investigations have focused on how size at migration varies during the settlement period (September-November). From these studies, it appears that size of post-larvae generally decreases during the settlement period (McDowall, 1968, McDowall and Eldon, 1980, McDowall, Mitchell and Brothers, 1994). Temporal studies on age at migration have documented the same trend, with post-larvae that migrate into freshwater in November being significantly younger than those migrating in September (McDowall *et al.*, 1994).

Variation in larval growth rates of migrating post-larvae has been examined for some whitebait species (September- January). A study in Victoria, Australia by Barbee *et al.* (2011), showed that īnanga larval growth rates increased significantly over the settlement



period. Pelagic larval duration decreased over the settlement period, as well as size at settlement. This research supported the findings of temporal studies completed in New Zealand and added insight into growth variability (McDowall, 1968, McDowall and Eldon, 1980, McDowall *et al.*, 1994).

Previous studies on post-larvae are limited in their ability to draw broad-scale conclusions because they only involved small spatial scales with limited sample sizes. Due to the highly heterogeneous oceanic conditions around New Zealand with extensive temporal variability, planktonic larvae of the five whitebait species returning to different regions will likely have experienced very different environmental conditions. Understanding how post-larvae in each region have responded to spatial and temporal variability in oceanic conditions will assist with developing a more comprehensive knowledge of New Zealand's whitebait species.

*The following questions were addressed in this chapter:*

- 1. Are there differences in age at migration of post-larval īnanga across the months of September, October and November?*
- 2. Are there differences in average daily pelagic growth rate of post-larval īnanga across the months of September, October and November?*

### **3.3 Methods and data analysis**

#### **3.3.1 Methods**

See Chapter 2, Section 2.3.

#### **3.3.2 Data analysis**

##### *Temporal variation in age at migration*

The age of 793 īnanga post-larvae sampled across New Zealand was compared among months (September, October and November). One-way ANOVAs were used to compare mean ages among months, and post hoc comparisons were completed with Tukey HSD tests.

##### *Temporal variation in larval growth rate*

Mean daily pelagic growth rate was calculated by averaging increment widths between daily rings. The mean growth rate of īnanga post-larvae was compared among months (September, October and November) using one-way ANOVAs. Post hoc comparisons were completed using Tukey HSD tests.

##### *Temporal variation in age – length relationship*

The age and length of 793 īnanga post-larvae entering rivers during the months September–November were used to calculate a age–length relationship. Spearman’s rank correlation was used to determine the relationship’s strength.

##### *Hatch date distribution*

All 793 īnanga collected in September– November 2015 were used to compile a distribution of hatch dates. The hatch date of individual fish was derived by subtracting its estimated age from the date of capture.

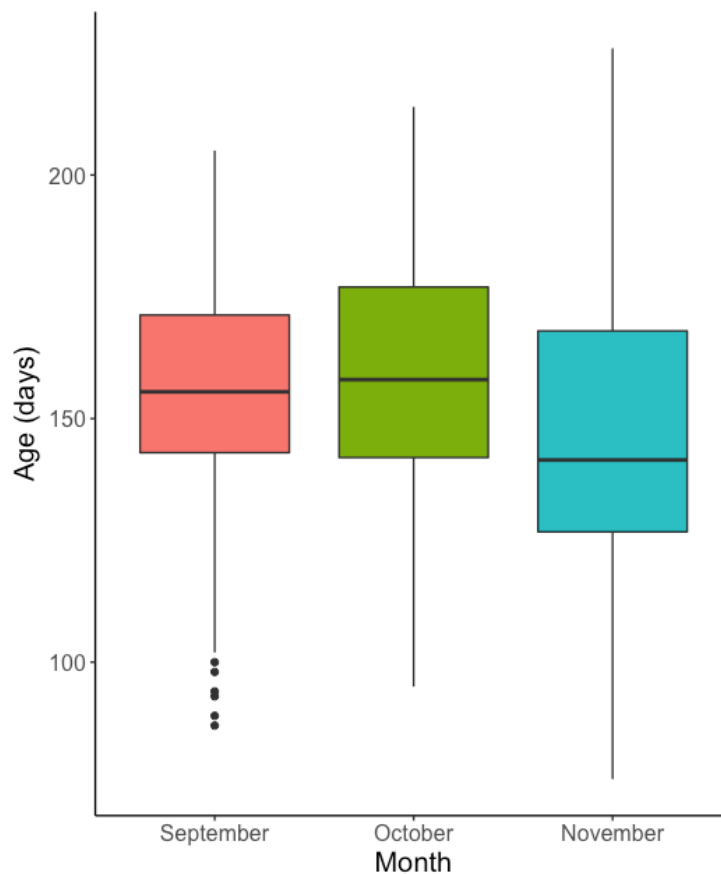
##### *Age-length relationship*

Spearman’s rank correlations were used to determine the strength of the relationship between age and length of īnanga. All īnanga collected in September 2015 were used to derive regional relationships and an overall age-length relationship.

## 3.4 Results

### 3.4.1 Overall temporal changes in age

Across all regions, the age of post-larval īnanga differed significantly among months ( $F_{2,790} = 14.84$ ,  $p < 0.05$ ; Fig. 3.3). Īnanga whitebait entering rivers during September ( $\bar{x} \pm \text{SE}$  age:  $156.3 \pm 1.6$  d) and October ( $157.4 \pm 2.2$  d) were significantly older than those entering during November ( $146.4 \pm 2.2$  d), but this pattern was not consistent across all regions or rivers.



**Figure 3.3.** Mean ( $\pm \text{SE}$ ) age of 793 post-larval īnanga collected during September, October and November 2015 from 20 rivers across eight regions of New Zealand. Box plots show the median, lower and upper quartiles (25% and 75%) and minimum and maximum values.

### 3.4.2 Temporal variation in age of whitebait within regions

The age of post-larval īnanga differed significantly between months for 12 out of 20 rivers. For nine of these rivers, the age of post-larval īnanga decreased significantly towards the end of the settlement period. For the remaining three rivers, the age of post-larval īnanga increased towards the end of the settlement period.

### *Bay of Plenty*

The age of post-larval īnanga entering the Kaituna River differed significantly between months ( $F_{2,38} = 12.89, p < 0.05$ ; Fig. 3.4). Post-larval īnanga entering the Kaituna River during September ( $\bar{x} \pm \text{SE age: } 118.2 \pm 6.1 \text{ d}$ ) were older than those entering in October ( $104.5 \pm 1.2 \text{ d}$ ); which in turn, were older than those entering during November ( $88.9 \pm 2.8 \text{ d}$ ).

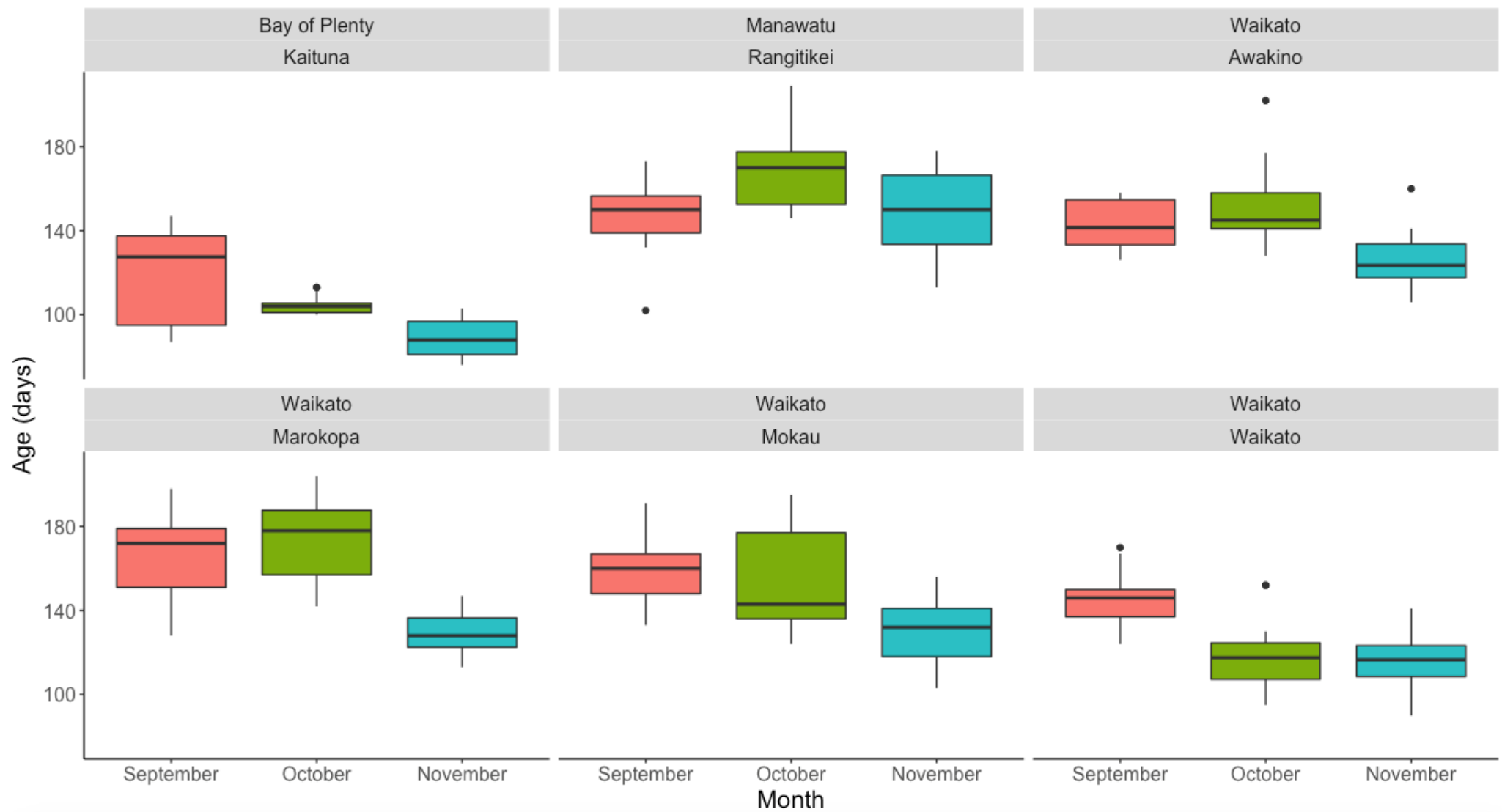
### *Waikato*

For all four rivers that were sampled in the Waikato region, there were significant differences between months in the age of post-larval īnanga. Īnanga whitebait entering the Mokau River ( $F_{2,40} = 7.991, p < 0.05$ ; Fig. 3.4) during September ( $\bar{x} \pm \text{SE age: } 160.4 \pm 4.4 \text{ d}$ ) and October ( $155.0 \pm 6.2 \text{ d}$ ) were older than those entering during November ( $131.8 \pm 4.8 \text{ d}$ ). Post-larval īnanga entering the Waikato River ( $F_{2,38} = 16.55, p < 0.05$ ; Fig. 3.4) during September ( $\bar{x} \pm \text{SE age: } 145.4 \pm 3.7 \text{ d}$ ) were older than those entering during October ( $118.6 \pm 4.7 \text{ d}$ ) and November ( $114.5 \pm 3.6 \text{ d}$ ).

For the other two rivers in the Waikato region, the age at migration of īnanga whitebait also decreased towards the end of the settlement period, but the oldest post-larval īnanga were found in October and not September. For the Awakino River ( $F_{2,40} = 10.94, p < 0.05$ ; Fig. 3.4), īnanga whitebait entering during November ( $\bar{x} \pm \text{SE age: } 126.1 \pm 3.8 \text{ d}$ ) were younger than those in September ( $143.4 \pm 3.2 \text{ d}$ ) and October ( $152.9 \pm 4.9 \text{ d}$ ). For the Marokopa River ( $F_{2,38} = 28.09, p < 0.05$ ; Fig. 3.4), post-larval īnanga sampled in November ( $\bar{x} \pm \text{SE age: } 129.7 \pm 2.8 \text{ d}$ ) were younger than those in September ( $167.2 \pm 5.7 \text{ d}$ ) and October ( $174.1 \pm 4.9 \text{ d}$ ).

### *Manawatu*

Īnanga whitebait entering the Rangitikei River ( $F_{2,41} = 5.973, p < 0.05$ ; Fig. 3.4) were older in October ( $\bar{x} \pm \text{SE age: } 168.6 \pm 4.5 \text{ d}$ ) than in September ( $147.1 \pm 4.4 \text{ d}$ ), but the average decreased in November ( $149.0 \pm 5.8 \text{ d}$ ).



**Figure 3.4.** Mean ( $\pm$ SE) age of post-larval īnanga collected during September, October and November 2015 from six rivers across three regions of the North Island, New Zealand. Box plots show the median, lower and upper quartiles (25% and 75%) and minimum and maximum values.

### *Tasman- Nelson*

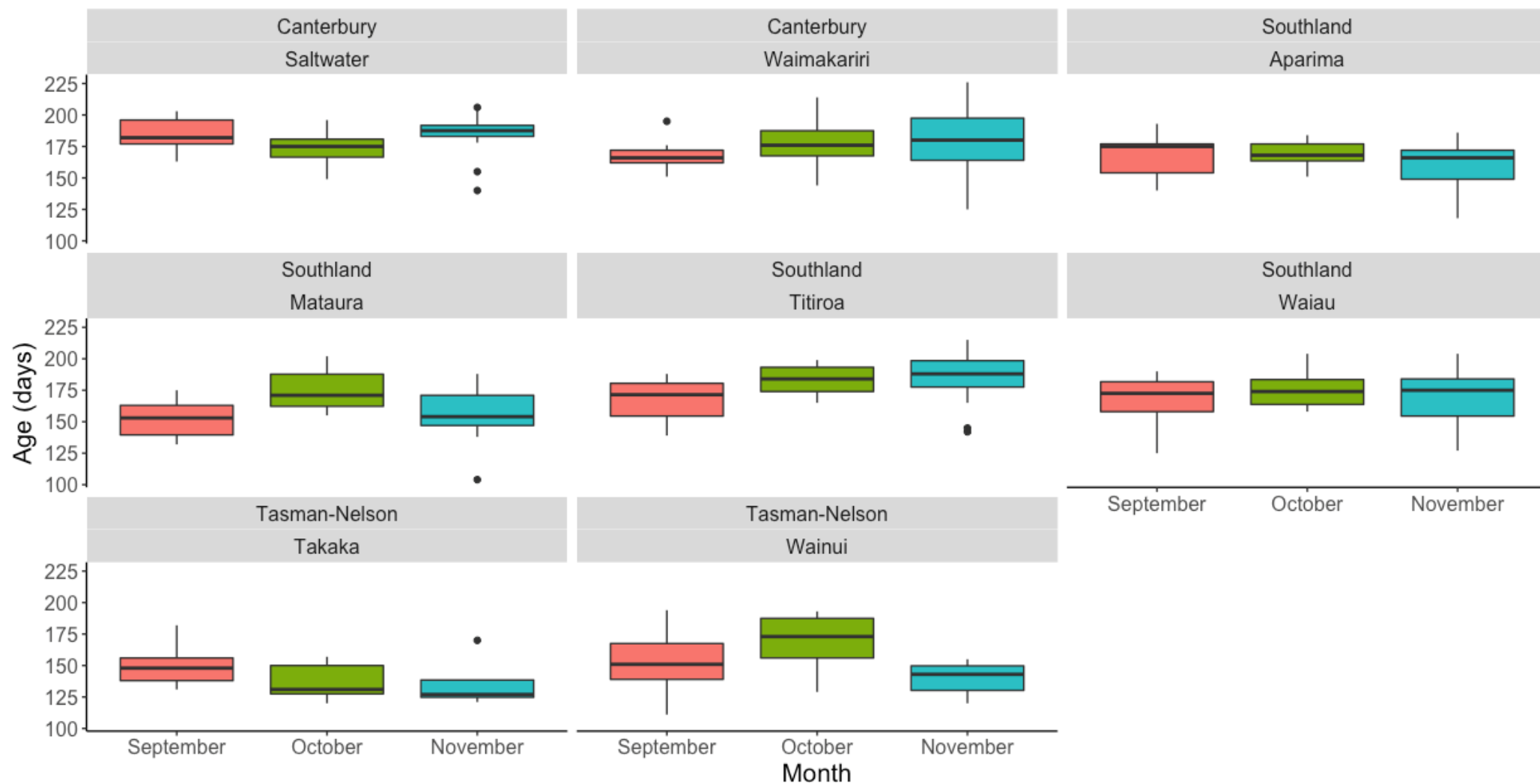
The age of post-larval īnanga entering the Takaka River did not differ significantly over the settlement period ( $F_{2,17} = 1.397, p = 0.274$ ; Fig. 3.7). For the Wainui River ( $F_{2,32} = 4.868, P < 0.05$ , Fig. 3.7), īnanga whitebait were older in October ( $\bar{x} \pm \text{SE}$  age:  $169.7 \pm 5.3$  d) than those entering in November ( $139.8 \pm 5.7$  d).

### *Canterbury*

Post-larval īnanga in the Canterbury region were the oldest fish found during the study. However, the ages of post-larvae entering the Waimakariri River ( $F_{2,38} = 1.052, p = 0.359$ ; Fig. 3.5) and Saltwater Creek ( $F_{2,40} = 3.172, p = 0.052$ ; Fig. 3.5) did not differ significantly among months. The mean age of īnanga whitebait in the Waimakariri was  $175.8 \pm 3.3$  d, but ages were very variable ranging from 145 - 226 d. The mean age across months for īnanga whitebait entering Saltwater creek was  $180.3 \pm 2.2$  d and ranged from 140 -206 d.

### *Southland*

From the four rivers within the Southland region only two showed significant variations in age of post-larvae among months. Īnanga whitebait entering the Titiroa River ( $F_{2,38} = 4.77, p < 0.05$ ; Fig. 3.5) in September ( $\bar{x} \pm \text{SE}$  age:  $167.3 \pm 4.2$  d) were younger than those in November ( $185.7 \pm 5.6$  d). Īnanga whitebait entering the Mataura River ( $F_{2,36} = 6.332, p < 0.05$ ; Fig. 3.5) during September ( $\bar{x} \pm \text{SE}$  age:  $152.5 \pm 4.5$  d) and November ( $155.6 \pm 6.2$  d) were younger than those in October ( $175.3 \pm 4.1$  d).



**Figure 3.5.** Mean ( $\pm$ SE) age of post-larval inanga collected during September, October and November 2015 from eight rivers across three regions of New Zealand. Box plots show the median, lower and upper quartiles (25% and 75%) and minimum and maximum values.

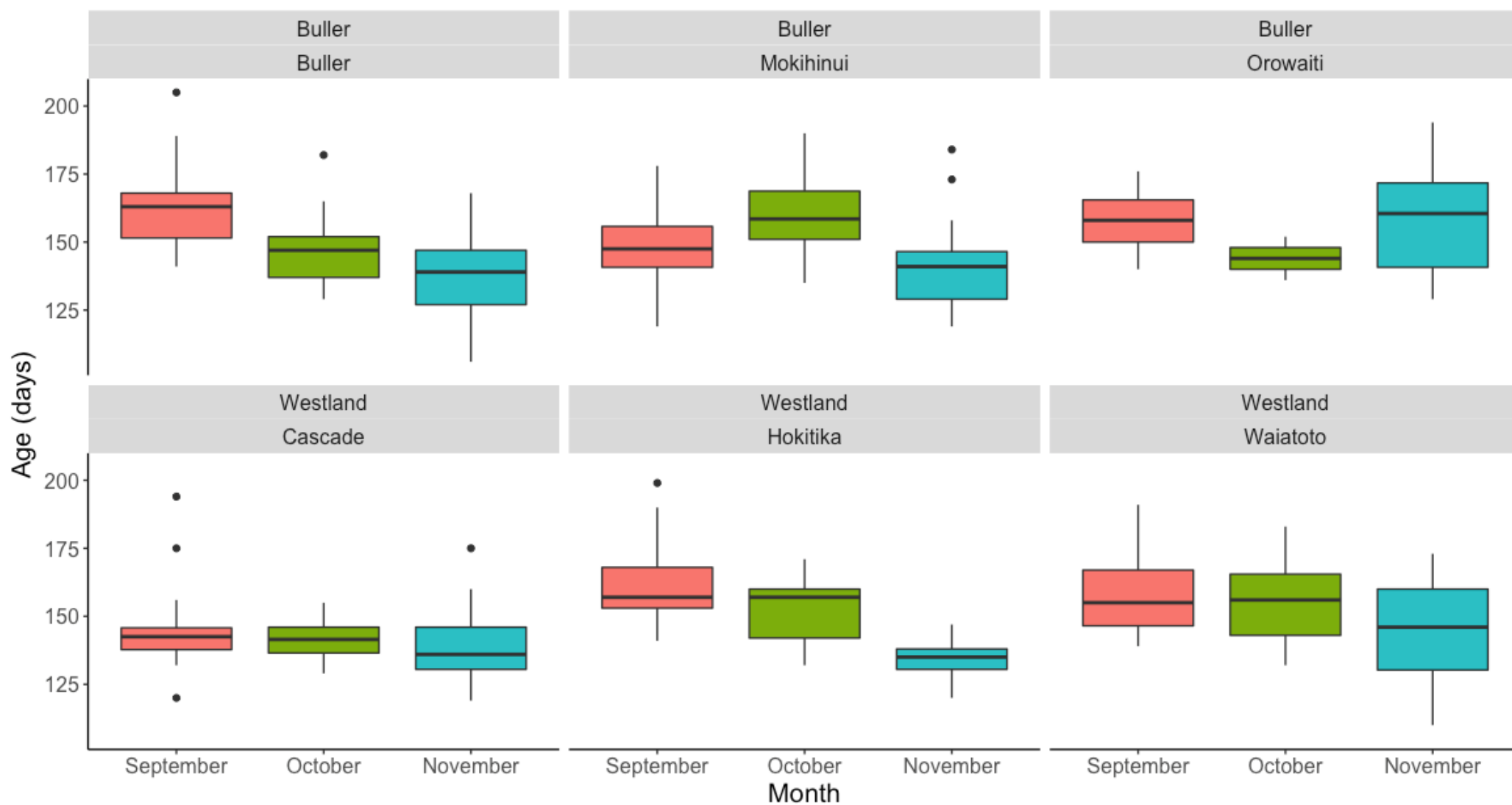
### *Buller*

The ages of īnanga whitebait differed between months for two of the three rivers within the Buller region. Post-larval īnanga entering the Mokihinui River ( $F_{2,44} = 5.069$ ,  $p < 0.05$ ; Fig. 3.6) were younger in November ( $\bar{x} \pm \text{SE age: } 142.1 \pm 4.7 \text{ d}$ ) than those in October ( $160.1 \pm 3.7 \text{ d}$ ). īnanga whitebait entering the Buller River ( $F_{2,42} = 10.41$ ,  $p < 0.05$ ; Fig. 3.6) in September ( $\bar{x} \pm \text{SE age: } 163.3 \pm 4.4 \text{ d}$ ) were older than those entering during October ( $147.2 \pm 4.3 \text{ d}$ ) and November ( $137.1 \pm 4.1 \text{ d}$ ).

### *Westland*

īnanga whitebait entering the Hokitika River were significantly younger towards the end of the settlement period ( $F_{2,38} = 16.90$ ,  $p < 0.05$ ; Fig. 3.6). Fish entering in November ( $\bar{x} \pm \text{SE age: } 133.9 \pm 1.8 \text{ d}$ ) were younger than those entering during September ( $162.2 \pm 4.9 \text{ d}$ ) and October ( $151.5 \pm 3.6 \text{ d}$ ). There were no significant differences between months in age at migration for the remaining two rivers: Cascade ( $F_{2,40} = 0.662$ ,  $p = 0.521$ ; Fig. 3.6) and Waiatoto ( $F_{2,37} = 2.125$ ,  $p = 0.134$ ; Fig. 3.6).

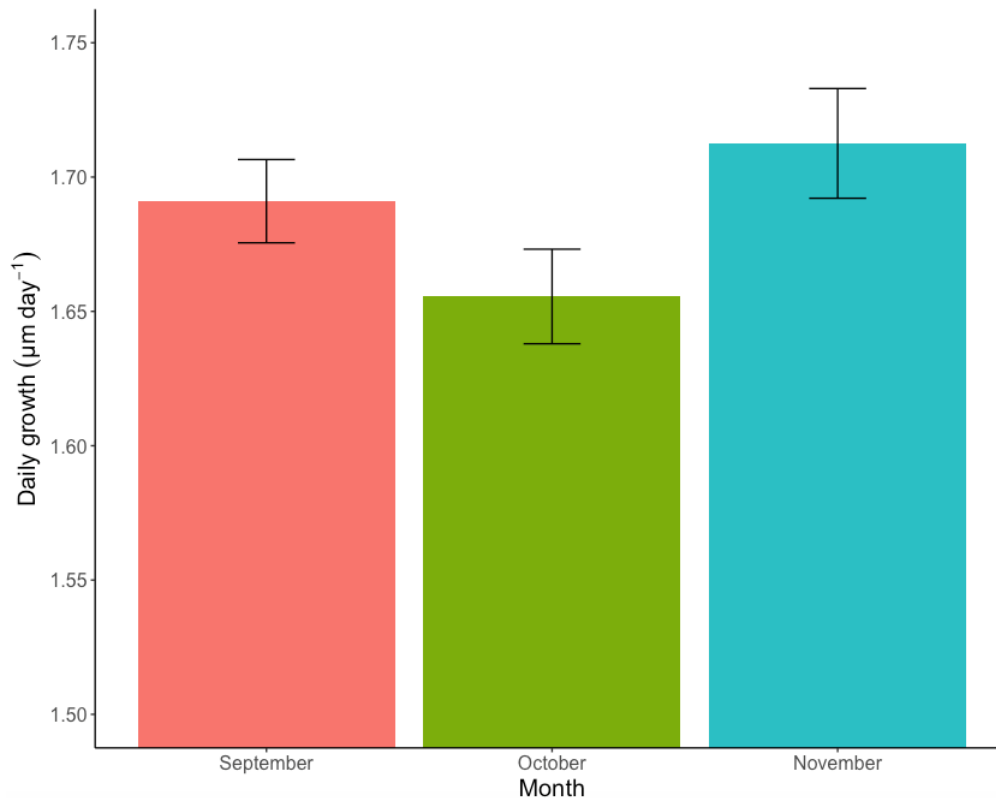




**Figure 3.6.** Mean ( $\pm$ SE) age of post-larval īnanga collected during September, October and November 2015 from six rivers across two regions of New Zealand. Box plots show the median, lower and upper quartiles (25% and 75%) and minimum and maximum values.

### 3.4.3 Overall temporal changes in mean daily growth rate

When comparing daily pelagic growth rate of īnanga entering rivers at differing times during the settlement period, trends found growth rate to be higher at the end of the period. Although daily growth rate was found to be higher in fish entering during the end of the settlement period, growth rate did not differ significantly between the months September–November ( $F_{2,788} = 2.57, p = 0.077$ ; Fig. 3.7).



**Figure 3.7.** Mean ( $\pm$ SE) daily pelagic growth rate of 793 post-larval *Galaxias maculatus* collected during September, October and November 2015 from 20 rivers across eight regions of New Zealand.

### 3.4.4 Temporal variation in mean daily growth rate

#### *Bay of Plenty*

The mean daily growth rate of post-larval īnanga entering the Kaituna River ( $F_{2,38} = 11.98, p < 0.05$ ; Fig. 3.8) during September ( $\bar{x} \pm \text{SE}$  growth:  $2.0 \pm 0.1 \mu\text{md}^{-1}$ ) was lower than those entering in October ( $2.2 \pm 0.1 \mu\text{md}^{-1}$ ) and November ( $2.3 \pm 0.1 \mu\text{md}^{-1}$ ).

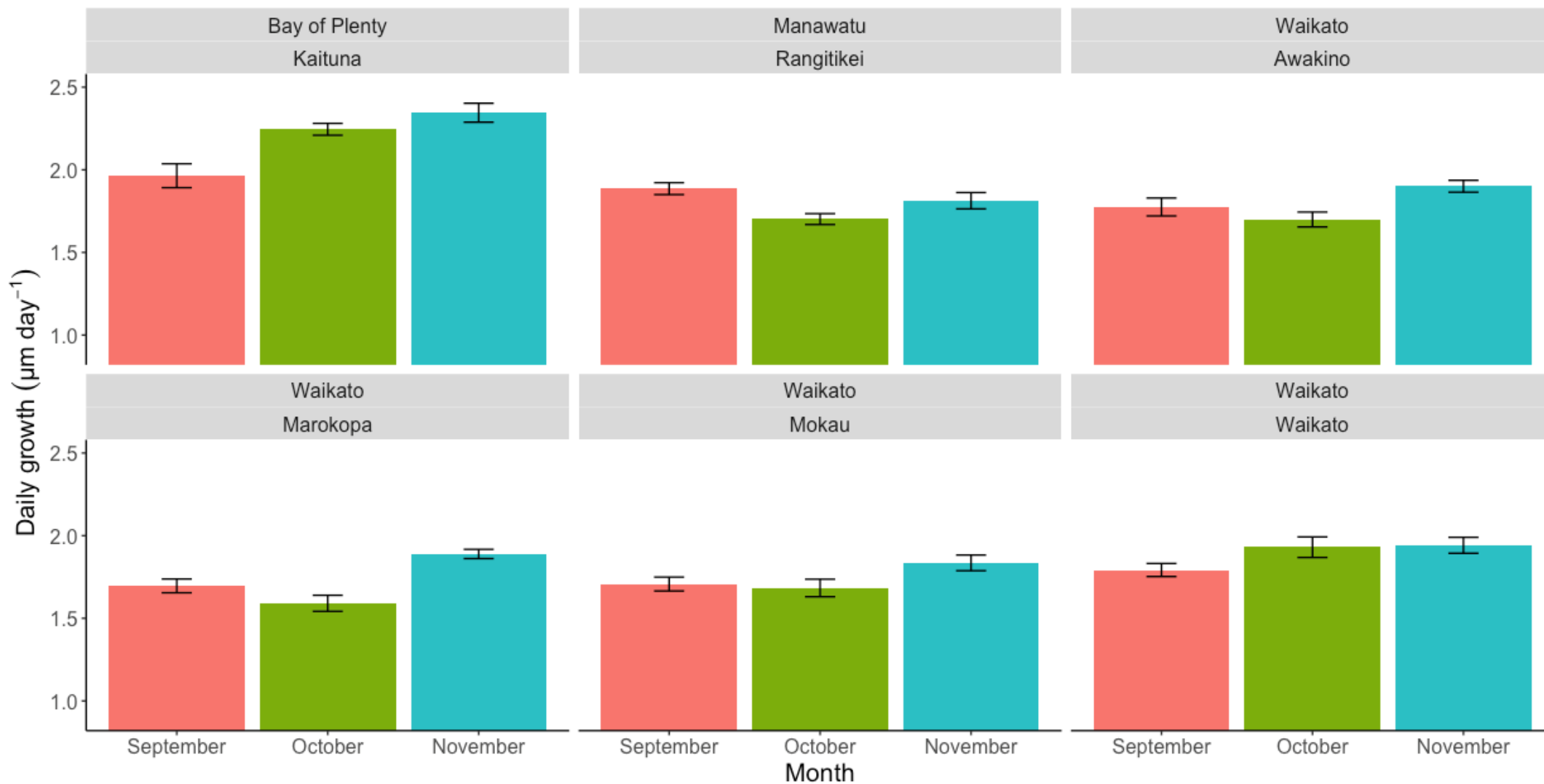
### *Waikato*

Only two of the four Waikato rivers had temporal differences in mean daily growth rate.

Post-larval īnanga in the Awakino River ( $F_{2,40} = 5.0, p < 0.05$ ; Fig. 3.8) that were captured in November had higher growth rates ( $\bar{x} \pm \text{SE growth: } 1.90 \pm 0.04 \mu\text{md}^{-1}$ ) than those entering during October ( $1.70 \pm 0.05 \mu\text{md}^{-1}$ ). In the Marokopa River ( $F_{2,38} = 14.49, p < 0.05$ ; Fig. 3.8), post-larval īnanga captured in November ( $\bar{x} \pm \text{SE growth: } 1.89 \pm 0.03 \mu\text{md}^{-1}$ ) had higher growth rates than those entering during September ( $1.70 \pm 0.04 \mu\text{md}^{-1}$ ) and October ( $1.59 \pm 0.03 \mu\text{md}^{-1}$ ). There were no temporal differences in the mean daily growth rate of post-larval īnanga entering the Mokau ( $F_{2,40} = 2.78, p = 0.0742$ ; Fig. 3.8) or the Waikato ( $F_{2,38} = 2.55, p = 0.091$ ; Fig. 3.8) Rivers.

### *Manawatu*

The mean daily growth rate of īnanga whitebait in the Rangitikei River differed significantly between months of capture ( $F_{2,41} = 5.607, p < 0.05$ ; Fig. 3.8). Growth was highest for fish caught in September ( $\bar{x} \pm \text{SE growth: } 1.89 \pm 0.03 \mu\text{md}^{-1}$ ) and lowest for those caught in October ( $1.70 \pm 0.03 \mu\text{md}^{-1}$ ).



**Figure 3.8.** Mean ( $\pm\text{SE}$ ) Daily pelagic growth of post-larval *Galaxias maculatus* collected during September, October and November 2015 from 6 rivers across three regions of New Zealand.

*Tasman- Nelson*

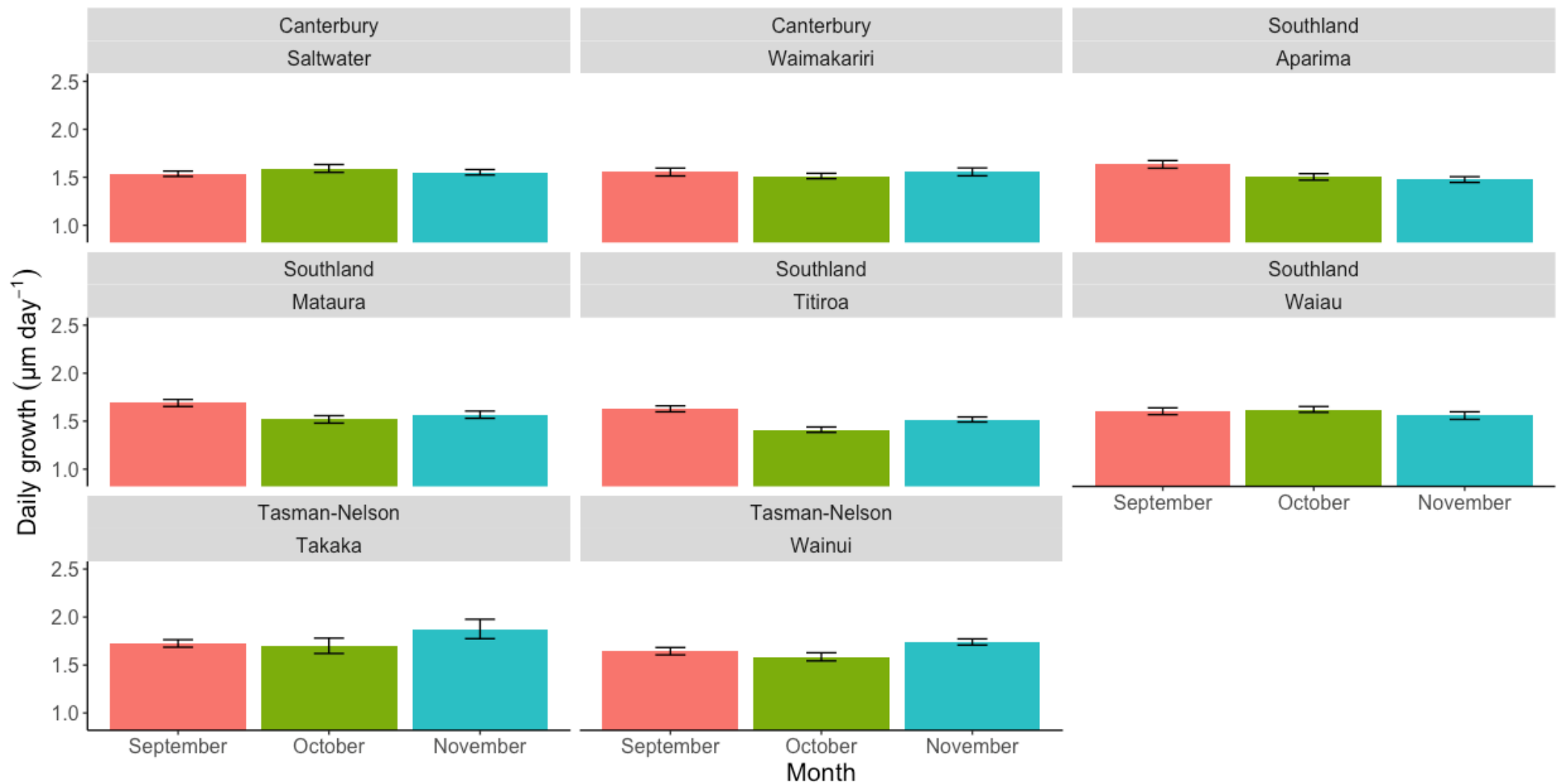
No significant differences in the average daily pelagic growth rate for post-larval inanga were found for the Takaka River ( $F_{2,17} = 1.46, P = 0.26$ ; Fig. 3.9) or Wainui River ( $F_{2,32} = 2.43, P = 0.104$ ; Fig. 3.9) between the months of September, October and November.

*Canterbury*

No significant differences in the average daily pelagic growth rate for post-larval inanga were found for the Waimakariri River ( $F_{2,38} = 0.459, P = 0.635$ ; Fig. 3.9) or Saltwater Creek ( $F_{2,40} = 0.748, P = 0.48$ ; Fig. 3.9) between the months of September, October and November.

*Southland*

Of the four rivers sampled within the Southland region, three showed significant differences in growth rate among months (September, October and November). In Maitai River ( $F_{2,36} = 5.284, P < 0.05$ ; Fig. 3.9) growth rate was highest in September ( $\bar{x} \pm SE$  growth:  $1.69 \pm 0.04$ ) and lowest in October ( $1.52 \pm 0.04$ ). In Aparima River ( $F_{2,28} = 5.69, P < 0.05$ ; Fig. 3.9) growth rate decreased over the settlement period recorded growths of  $1.63 \pm 0.04$  in September,  $1.50 \pm 0.03$  in October and  $1.48 \pm 0.03$  in November. Titiroa River ( $F_{2,38} = 13.61, P < 0.05$ ; Fig. 3.9) growth rate followed a similar trend to Maitai and Aparima River where growth rate in September ( $\bar{x} \pm SE$  growth:  $1.63 \pm 0.03$ ) was higher than those entering during October ( $1.42 \pm 0.03$ ) and November ( $1.52 \pm 0.03$ ).



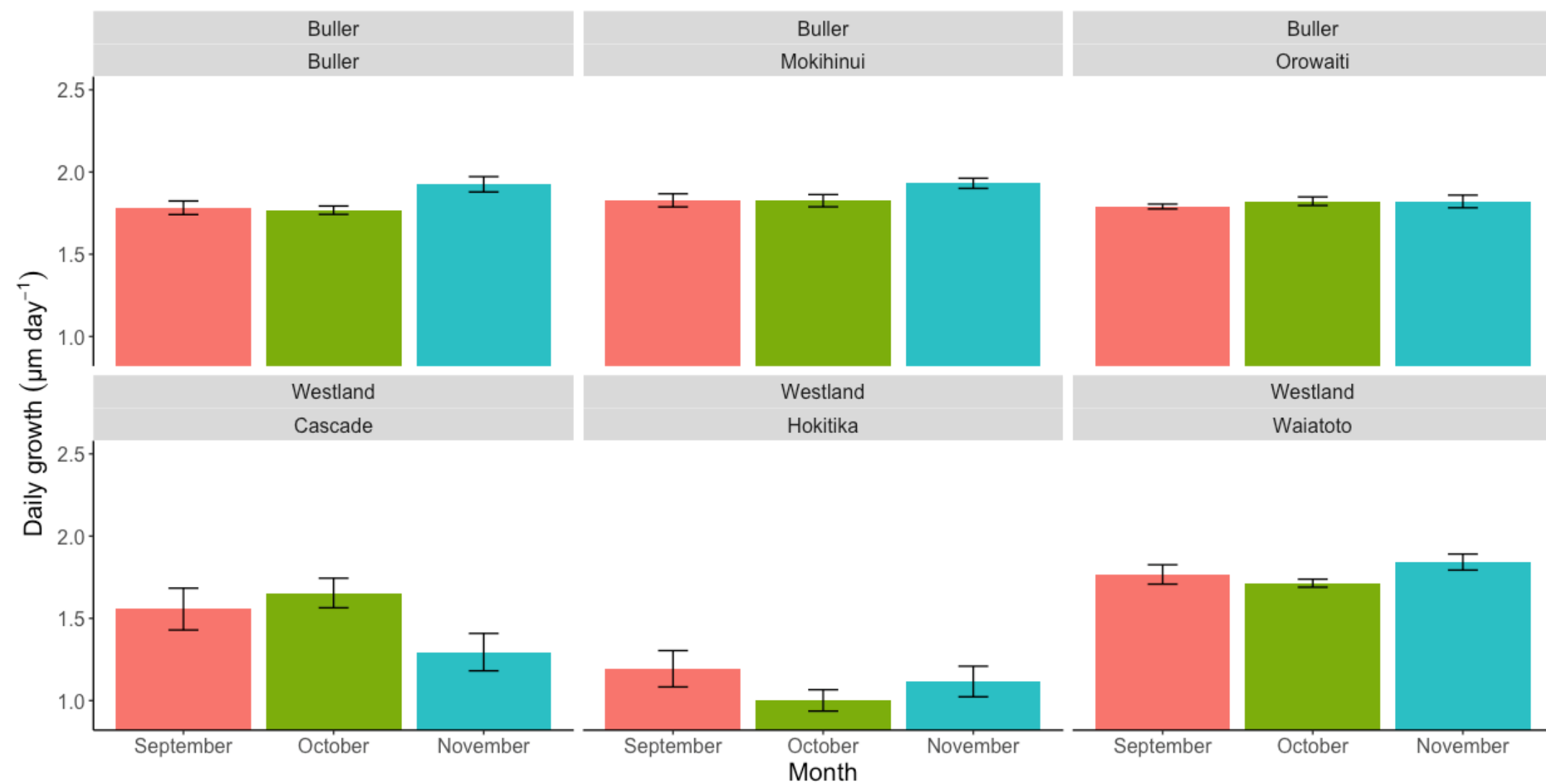
**Figure 3.9.** Mean daily growth rate ( $\pm$ SE) of post-larval īnanga collected during September, October and November 2015 from eight rivers across three regions of New Zealand.

### *Buller*

When comparing mean daily growth rates of post-larval īnanga captured in rivers in the Buller region, only the Buller River ( $F_{2,40} = 4.83, p = 0.0132$ ; Fig. 3.10) showed differences between months. Post hoc comparisons showed the mean daily growth of post-larval īnanga caught in November ( $\bar{x} \pm \text{SE growth: } 1.93 \pm 0.05 \mu\text{md}^{-1}$ ) was higher than that of post-larval īnanga caught in September ( $1.78 \pm 0.16 \mu\text{md}^{-1}$ ) and October ( $1.77 \pm 0.09 \mu\text{md}^{-1}$ ). Post-larval īnanga entering the Mokihinui ( $F_{2,44} = 2.70, p = 0.0782$ ; Fig. 3.10) and Orowaiti River ( $F_{2,28} = 0.33, p = 0.722$ ; Fig. 3.10) did not show any temporal differences in mean daily growth rates.

### *Westland*

The mean daily growth rates of post-larval īnanga in all three rivers sampled in the Westland region, Hokitika ( $F_{2,38} = 1.062, P = 0.356$ ; Fig. 3.10), Cascade ( $F_{2,40} = 2.837, p = 0.0704$ ; Fig. 3.10) and Waiatoto River ( $F_{2,37} = 2.359, p = 0.109$ ; Fig. 3.10) did not differ between month of capture. īnanga whitebait entering the Waiatoto River appeared to have higher mean daily growth rates in most months than the other two Westland rivers.

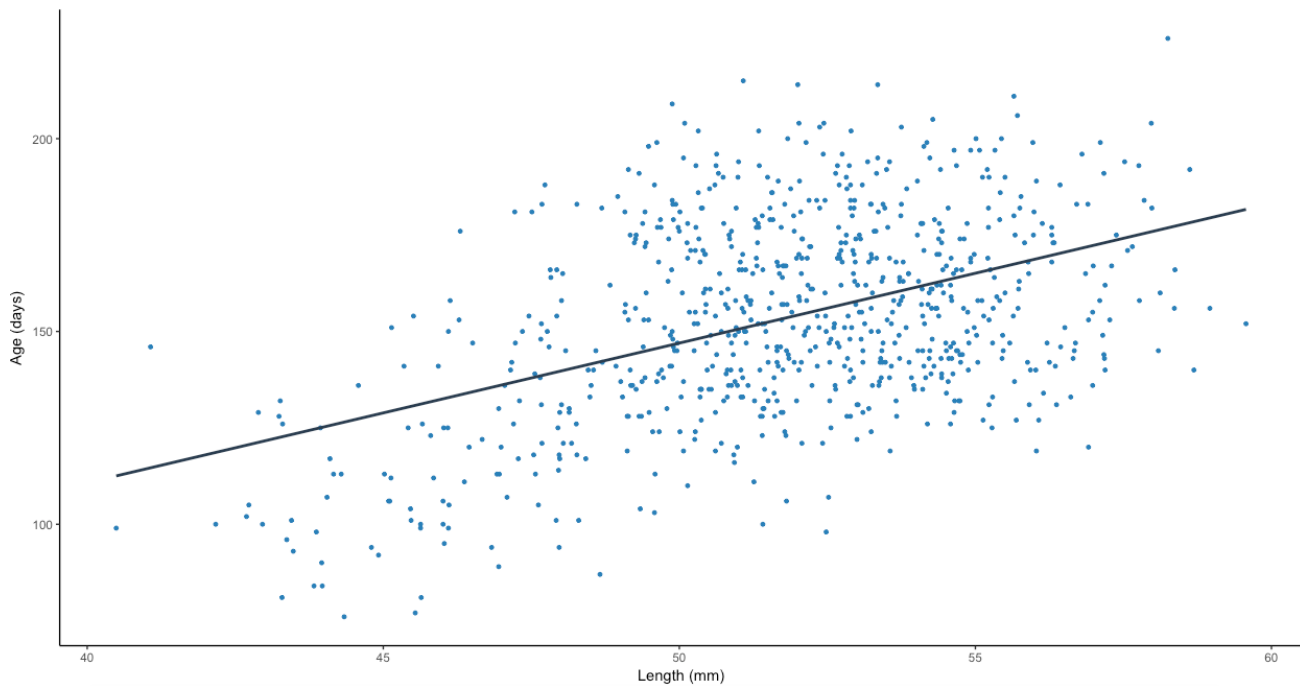


**Figure 3.10.** Mean daily growth rate ( $\pm$ SE) of post-larval īnanga collected during September, October and November 2015 from six rivers across two regions of New Zealand.



### 3.4.5 Age-length relationship

Post-larval īnanga ( $n=793$ ) sampled in September, October and November were used to investigate the relationship between age and length. The overall relationship showed a weak, positive correlation ( $r_s = 0.35, p < 0.05$ ; Fig. 3.11). The strength and significance of the association between age and length differed between regions and month of capture (Table. 3.1).



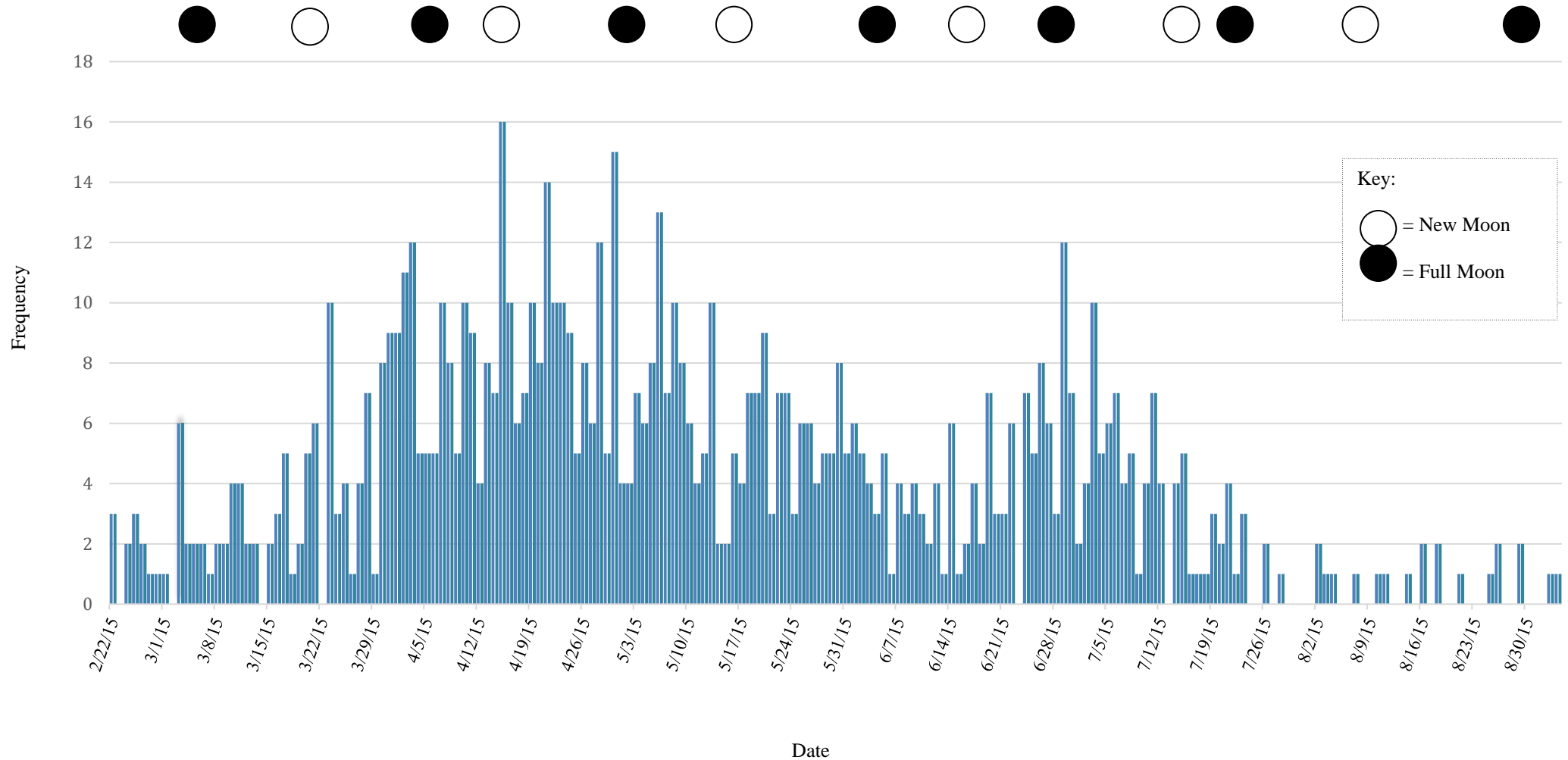
**Figure 3.11.** Age – length relationship of 793 post- larval īnanga entering 20 rivers within eight regions of New Zealand during September, October and November 2015.

**Table 3.1.** Spearman’s correlation results for age and length of īnanga whitebait entering differing regions of New Zealand during September, October and November. NS denotes a non-significant result, (\*) denotes a significant value at the  $p < 0.05$  level.

Region	Spearman’s Correlation		
	September	October	November
Bay of Plenty	$r = 0.12$ , NS	$r = -0.19$ , NS	$r = 0.09$ , NS
Waikato	$r = 0.23$ , NS	$r = 0.52^*$	$r = 0.39^*$
Manawatu	$r = 0.16$ , NS	$r = -0.11$ , NS	$r = 0.34$ , NS
Tasman/Nelson	$r = 0.37$ , NS	$r = 0.36$ , NS	$r = 0.15$ , NS
Canterbury	$r = 0.33$ , NS	$r = 0.42^*$	$r = 0.39^*$
Southland	$r = 0.21$ , NS	$r = -0.06$ , NS	$r = 0.24$ , NS
Buller	$r = -0.34^*$	$r = 0.15$ , NS	$r = 0.52^*$
Westland	$r = 0.04$ , NS	$r = 0.66^*$	$r = 0.42^*$

### **3.4.6 Hatch date distribution**

Hatch date distributions were calculated for post-larval īnanga collected during September, October and November 2015 (Fig. 3.12). Back calculated hatch dates showed that the majority of post-larval īnanga hatched during autumn (March 13%, April 33% and May 24%). The highest frequency of post-larval īnanga being born on one particular day was 16 on 15/04/15. When comparing the hatch date distributions against moon phase for the year 2015 it is evident that pulses of hatching occurred directly after new and full moons throughout the year (Table 3.2).



**Figure 3.12.** Hatch date distribution of post-larval īnanga (*G. maculatus*) from 20 rivers in New Zealand. Samples were collected during September, October and November 2015 (n=793). Also shown are lunar phases (full and new moons) for 2015. Hatch dates were derived from age estimates of otoliths.

### 3.5 Discussion

The age of post-larval īnanga tended to decrease during the settlement period (September–November), while the average daily pelagic growth rate increased. For example, post-larval īnanga entering the Kaituna River in September were older with lower average daily growth rates than those entering in November. These results are in agreement with the findings of McDowall *et al.* (1994) and Barbee *et al.* (2011) who found significant reductions in age and increases in daily pelagic growth for fish entering rivers in New Zealand and Australia later in the year.

As suggested in Section 2.6 the likely drivers of variability seen in īnanga early life history traits is a response to localised oceanic conditions such as sea surface temperature (SST) and productivity (Houde, 1989). Seasonal variability in oceanic conditions has been shown to directly influence larval growth of marine species via its effect on growth efficiency, oxygen uptake, food consumption and metabolic rate (Houde, 1989, Trip *et al.*, 2014).

The seasonal change in age and growth documented in my study coincides with seasonal fluctuations in SST around New Zealand. In general, SST warms across September, October and November. For example, the Waikato and Bay of Plenty regions are characterized by large seasonal fluctuations in sea temperature (e.g. annual amplitude in SST is c. 4°C) (Chiswell, 1994) and post-larval īnanga were younger with higher growth rates. Productivity in these regions is characterized by “spring blooms” where a peak is seen in September with large reductions in productivity thereafter (Murphy *et al.*, 2001). It is likely then, that seasonal fluctuations in SST is responsible for the temporal trends seen in these regions. Post-larval īnanga collected from the Kaituna River in November (mean age = 88d) would have begun their pelagic larval development 88 days earlier as primary productivity was increasing to a spring peak. As this increasing productivity flowed through the food chain to larger zooplankton it would have closely matched the changing needs of the developing larvae. This would likely have resulted in greater daily growth rates and faster development resulting in younger post-larvae. Post-larval īnanga captured in the same river in September would have developed during winter, in a less productive oceanic environment, had slower growth rates and development, resulting in older post-larvae.

The trend for most regions during the settlement period was an increase in average daily growth rate and shorter larval duration for īnanga. However, for some rivers and regions (e.g. Manawatu, Canterbury and Southland) there was little or no temporal variation in age at migration or average daily growth. It is likely that this lack of variation is due to the lower and more constant SST and productivity that characterizes these regions (Egan 2017).

The regional trends in age and growth described above are supported by recent research by Egan (2017) who also found inanga whitebait from different regions displaying different temporal responses in early life history traits. Egan (2017) also found very little temporal variability in the growth of īnanga in regions such as Canterbury and concluded that temporal biotic drivers were weaker in this area. The results from this study and Yungnickel (2017) further highlight the importance of differences occurring in regional populations within the whitebait fishery spatially and temporally.

My study found a positive but weak relationship between age and length in īnanga whitebait. This suggests that larger post-larvae are generally older. Although my study aged many post-larvae, this relationship can be used to better interpret the results of McDowall (1968) who, with much larger sample sizes, found larger whitebait entering rivers at higher latitudes such as the Westland region. Coupled with the age and growth trends documented in my study it is clear that īnanga whitebait at higher latitudes in New Zealand are slower growing fish that are older and larger at migration.

The hatch date distributions of fish sampled in my study revealed that the majority of īnanga whitebait entering rivers around New Zealand in spring had hatched during autumn. Hatch dates often coincided with full and new moons. These results add further support to studies such as McDowall and Eldon (1980) and Sigman and Hain (2012) that found īnanga hatching peaked during full and new moons because the associated spring tides caused re-immersion and hatching of fully developed eggs.

## **Chapter 4: Early life history traits of the less common whitebait species kōaro, banded kōkopu, giant kōkopu and shortjaw kōkopu**

### **4.1 Summary**

- Kōaro and banded kōkopu whitebait entering rivers at lower latitudes were younger and had higher average daily pelagic growth rates than whitebait entering rivers at higher latitudes.
- Banded kōkopu whitebait ( $\bar{x}$  = 106.2 d) were younger than kōaro whitebait (138.3 d).
- Giant kōkopu whitebait were 131 d old on average.
- The average age of the two shortjaw kōkopu whitebait was 152 d.
- Hatch dates for kōaro, banded kōkopu and giant kōkopu occurred between April and August with kōaro displaying peaks during May and June and banded kōkopu displaying peaks at the end of June/start of July.

### **4.2 Introduction**

The organised aggregation of individuals, known as ‘shoaling’, has been documented regularly in marine species. It is estimated to occur in around 10,000 species of fish at some point of their life cycle and provides benefits and costs to species that cooperate in the behavior (Shaw, 1978). The benefits associated with fish aggregations include increased foraging opportunity, reductions in the per capita rate of predation and reduced energy expenditure from swimming. With benefits come costs, shoaling species are more likely to incur predator encounters and are subject to higher levels of competition than an isolated individual (Pavlov and Kasumyan, 2000, Ward, Axford and Krause, 2002).

Shoals are usually composed of single species, although there is limited evidence of heterospecific adults exhibiting the behavior. However, mixed-species shoaling by flatiron herring (*Harengula thrissina*) and anchovetas (*Cetengraulis mysticetus*) was recorded by Hobson (1963). Parrish (1989) recorded silverside (*Allanetta harringtonensis*), round herring (*Jenkinsia lamprotaenia*), anchovy (*Anchoa choerostoma*), and pilchard (*Harengula humeralis*) shoaling in Bermuda.

Unlike adult fish, heterospecific shoaling of juveniles is widespread and has been documented frequently. For example, several species of juvenile parrotfish (*Scaridae*) were documented shoaling by Overholtzer and Motta (2000) in the Florida Keys, and shoals of common minnow (*Phoxinus phoxinus*) often contain common roach (*Rutilus rutilus*), dace (*Leuciscus leuciscus*) and sunbleak (*Leucaspisus delineatus*) (Soin, Kasutyan and Pashchenko, 1981). Additionally, shoals of juvenile golden shiner (*Notemigonus crysoleucas*) often include fish from four other species (*Fundulus diaphanus*, *Castostomus commersonii*, *Gasterosteus aculeatus*, and *A. quadratus*; Krause, Godin and Brown, 1996). These heterospecific shoals are a result of the juveniles having similar biology and habitat preferences, and lacking lengthy migrations (Pavlov and Kasumyan, 2000). Species that are less abundant in shoals tend to be at more of a disadvantage with regards to predation especially if the specie is morphologically dissimilar (Parrish, 1989). In New Zealand, shoals of whitebait are composed of a mix of juveniles of five diadromous species of Galaxiids (McDowall, 1968).

Due to the uncommonness of heterospecific shoaling in adult fish, specifications on how to manage fisheries that target mixed shoals do not exist. For the New Zealand whitebait fishery, nationwide regulations (see Section 1.1.5) are applied to all five species despite variations in abundance, habitat preferences, spawning patterns, age and size at migration (McDowall, Mitchell and Brothers, 1994, Allibone and Caskey, 2000, Bonnett and Sykes, 2002).

Historical literature on the early life history traits of whitebait has focused on īnanga due to this species' dominance within the whitebait catch (McDowall, 1965, Yungnickel, 2017). McDowall *et al.* (1994) focused on all five whitebait species, but had limited spatial coverage and small sample sizes. They found that age at migration ranged from 93-128 d for banded kōkopu (n=44), 110-155 d for kōaro (n=70), 113-137 d for giant kōkopu (n=10) and 120-136 d for shortjaw kōkopu (n=5). Peak spawning took place in April to mid-May for banded kōkopu and kōaro, and mid-June for giant kōkopu and shortjaw kōkopu. Early life history traits of the four remaining species are believed to follow similar trends to that of īnanga, with age and size of whitebait declining towards the end of the main settlement period (September- November).

McDowall and Kelly (1999) followed on from the seminal work carried out by McDowall *et al.* (1994), but focused purely on giant kōkopu. They used information from McDowall *et al.* (1994) and aged an additional 107 giant kōkopu from nine rivers. They found that spawning occurred between June and August with age at migration ranging from 104-140 d. Shortjaw kōkopu make up the smallest proportion of the whitebait catch and are often overlooked in whitebait studies due to their paucity and difficulties with identification (Yungnickel, 2017). A study by Allibone, Caskey and Miller (2003) observed adults in a small stream in the Mt Taranaki National Park. They observed spawning between late April and early May with eggs hatching in late May.

It is apparent that there are gaps in background knowledge about the four less common whitebait species. Like īnanga, studies are largely limited by sample sizes and spatial coverage, for example, only 44 banded kōkopu from 6 rivers were aged by McDowall *et al.* (1994). Although this is likely due to paucity of these less common species, it is important to understand the early life history traits of these species and assess any spatial or and temporal variability. To effectively manage the whitebait fishery and for the conservation of all of its constituent species, an in depth understanding of the early life history of not only īnanga but all species that make up the whitebait catch is crucial. Limited knowledge of the remaining species, particularly spatial and temporal variability, could result in loss of individual species from the whitebait catch and local extinctions.

*The following questions were addressed in this chapter:*

1. *What is the age at migration of the four less common whitebait species?*
2. *Do these ages vary spatially or temporally?*
3. *What is the average daily pelagic growth rate of the four less common whitebait species?*
4. *Do these growth rates vary spatially and temporally?*
5. *What is the hatch date distribution of four less common whitebait species?*



## 4.3 Methods and data analysis

### 4.3.1 Methods

Full methods are described in Section 2.3.

### 4.3.2 Genetic testing for identification of shortjaw kōkopu whitebait

Due to the uncertainty of identifying shortjaw kōkopu within the whitebait catch, the species identities of the two shortjaw kōkopu used for aging was genetically confirmed. Yungnickel (2017) deployed genetic markers to confirm species identification; the methods were:

#### *DNA extraction*

DNA was extracted from caudal fin clips (1mm x 2mm) leaving the remainder of the fish intact and available for further morphological examining. Chelex 100 resin (BioRad) was used to extract DNA by placing the caudal fin tissue into 1.5ml tubes containing 400µl of 5% Chelex and 40mg proteinase K. The tubes were allowed to incubate overnight before being heated to 90°C for 10 minutes then centrifuged at ~20,000 x g for 10 minutes.

#### *PCR amplification and sequencing*

Approximately 1200bp of mitochondrial cytochrome b was amplified using primers situated in the flanking tRNAs; cytb-glu and cytb-thr (Waters *et al.*, 2001). PCRs contained 0.5µM each primer and 1 x MyFi Mix (Bioline) in a total volume of 10µl and were cycled in an Eppendorf Mastercycler Pro S thermocycler: 94°C for 120 s, followed by 35 cycles of 94°C for 30 s, 47°C for 30 s, 72°C for 60 s, with a final extension of 72°C for 240 s.

Two microliters of amplified DNA was visualized on a 1% agarose gel containing SYBR safe (Thermo Fisher) using blue LED transilluminator (UVI). The remaining DNA was purified using a MEGA quick-spin total fragment DNA purification kit (iNtRON) and quantified using a Nanodrop ND-1000 spectrophotometer (Thermo Fisher). Purified DNA was sequenced using primer cytb-glu on an ABI 3730xl DNA Analyser (Genetic Analysis Service, Department of anatomy, University of Otago), producing up to 930bp of usable sequence after editing.

### *Species identification*

Species identification was diagnosed using BLAST searches of the NCBI GenBank database (Altschul *et al.*, 1990), and confirmed by aligning the sequences to large dataset containing references sequences and subsequent Neighbour-Joining tree building.

### **4.3.3 Data analysis**

#### *Age at migration of the four less common whitebait species*

Age comparisons were made between each river sampled and, where possible, among rivers within regions. Temporal comparisons were between months the September, October, November and December where possible. Comparisons were carried out using simple one-way ANOVAs and post hoc comparisons were completed with Tukey HSD tests. The less common whitebait species were most abundant in the whitebait samples at differing times during the settlement period (Yungnickel 2017). Accordingly, spatial comparisons were made with samples collected in September 2015 for kōaro, October 2015 for banded kōkopu, November and December 2015 for giant kōkopu and November 2015 for shortjaw kōkopu.

#### *Daily pelagic growth rate of the four less common whitebait species*

Growth comparisons were made between each river sampled and, where possible, among rivers within regions. Temporal comparisons were made between the months of September, October, November and December where possible. Comparisons were made using simple one-way ANOVAs and post hoc comparisons were completed with Tukey HSD tests. The same monthly samples used for age comparisons (see above) were used for growth comparisons.

#### *Hatch date distributions of the four less common whitebait species*

Hatch date distributions were back-calculated for kōaro, banded kōkopu and giant kōkopu. Small sample sizes prevented hatch date distributions from being completed for shortjaw kōkopu. Hatch dates were calculated by subtracting the estimated age from the collection date (migration to freshwater).

## 4.4 Results

### 4.4.1 Age of kōaro and banded kōkopu whitebait

There was high variability in the age at migration of the 296 post-larval kōaro in samples. Sample means ranged from 125.4 d to 170.5 d (Fig. 4.1) with an overall average age of 138.3 days. Kōaro whitebait in samples from the Waiau River (170.5 d) in Southland were 22.4 days older on average than those from the river with the next highest sample mean, the Wanganui River (148.1 d) in Westland. There was large variation in age at migration of the 446 banded kōkopu whitebait in samples with sample means ranging from 46 d to 131.9 d, with the overall age averaging 106.2 days.

### 4.4.2 Spatial variation in age of kōaro whitebait

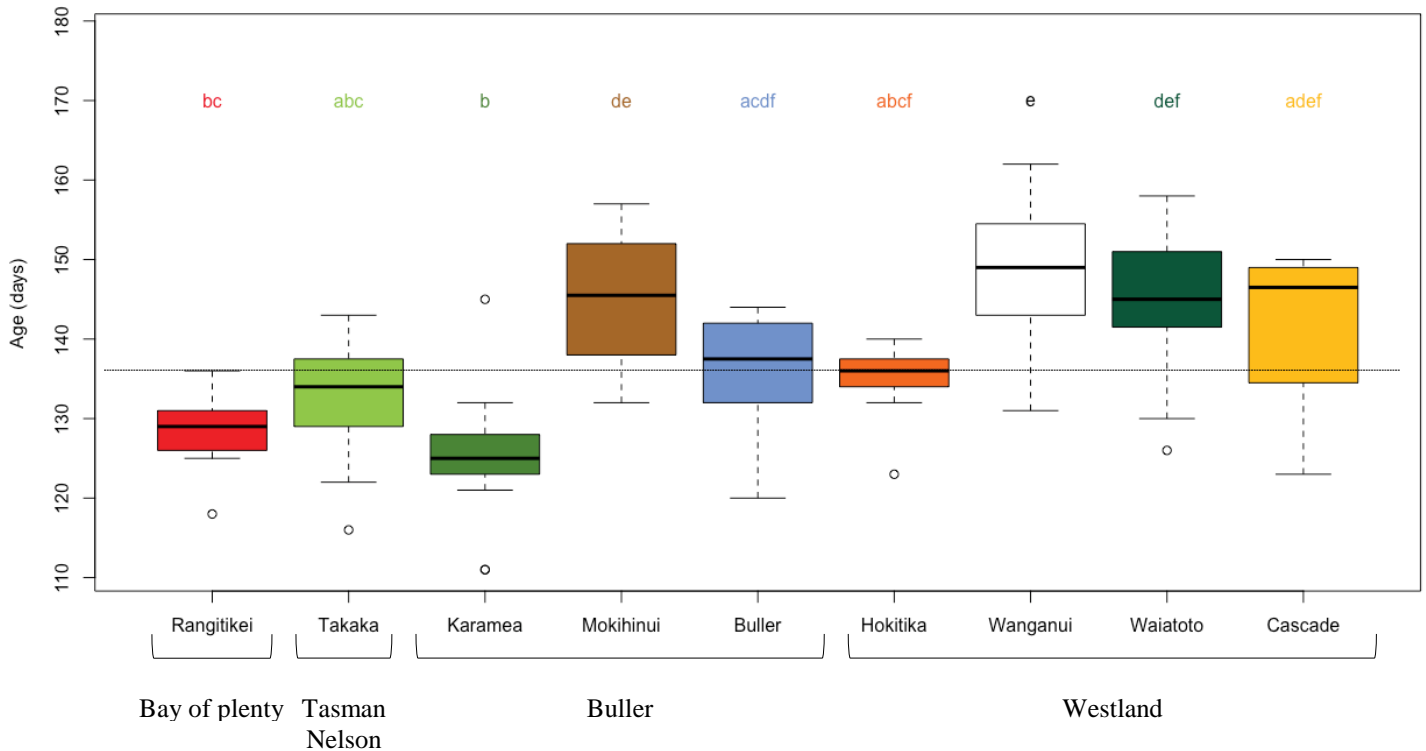
In September 2015, there were significant differences in the age of kōaro whitebait entering nine rivers across New Zealand ( $F_{8,100} = 11.9, p < 0.05$ ; Fig. 4.1). Kōaro entering rivers at lower latitudes in the North Island such as the Rangitikei River ( $\bar{x} \pm \text{SE age: } 128.2 \pm 1.5 \text{ d}$ ) were younger than those at higher latitudes in the South Island such as the Wanganui ( $148.1 \pm 3.9$ ) and Waikatoto ( $144.4 \pm 2.4$ ) Rivers.

#### *Buller*

There were significant differences in the age of kōaro whitebait entering three rivers in the Buller region ( $F_{2,40} = 11.18, p < 0.05$ ). Kōaro whitebait entering the Mokihinui River ( $\bar{x} \pm \text{SE age: } 145.3 \pm 2.2 \text{ d}$ ) were significantly older than those entering the Buller ( $135.9 \pm 1.9 \text{ d}$ ) and Karamea ( $132.3 \pm 1.9 \text{ d}$ ) Rivers.

#### *Westland*

In September 2015, there were significant differences in the age of post-larval kōaro entering four rivers in Westland ( $F_{2,37} = 3.82, p < 0.05$ ). Post hoc comparisons of kōaro whitebait entering the Hokitika River ( $\bar{x} \pm \text{SE age: } 135.0 \pm 1.4 \text{ d}$ ) were thirteen days younger on average than those in the Wanganui River ( $148.1 \pm 3.9 \text{ d}$ ).



**Figure 4.1.** Age at migration of kōaro whitebait (*G. brevipinnis*) entering nine rivers within New Zealand during September 2015. Boxes represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values. Different letters above boxes indicate rivers that are significantly different (Tukey's HSD,  $p < 0.05$ ). Dotted line denotes overall mean age.

#### 4.4.3 Spatial variation in age of banded kōkopu whitebait

In October 2015, there were significant differences in the age of banded kōkopu whitebait entering 16 rivers across New Zealand ( $F_{15,172} = 8.34$ ,  $p < 0.05$ , Fig. 4.2). Banded kōkopu post-larvae entering the Waikato River ( $\bar{x} \pm \text{SE}$  age:  $90.27 \pm 2.65$ ) were significantly younger than those collected from all but two (Mokau & Orowaiti) of the other rivers.

##### Waikato

Banded kōkopu whitebait entering the four rivers within the Waikato region (Waikato, Marokopa, Waikawau and Mokau) did not differ significantly in age ( $F_{2,32} = 1.59$ ,  $p = 0.22$ ).

##### Tasman- Nelson

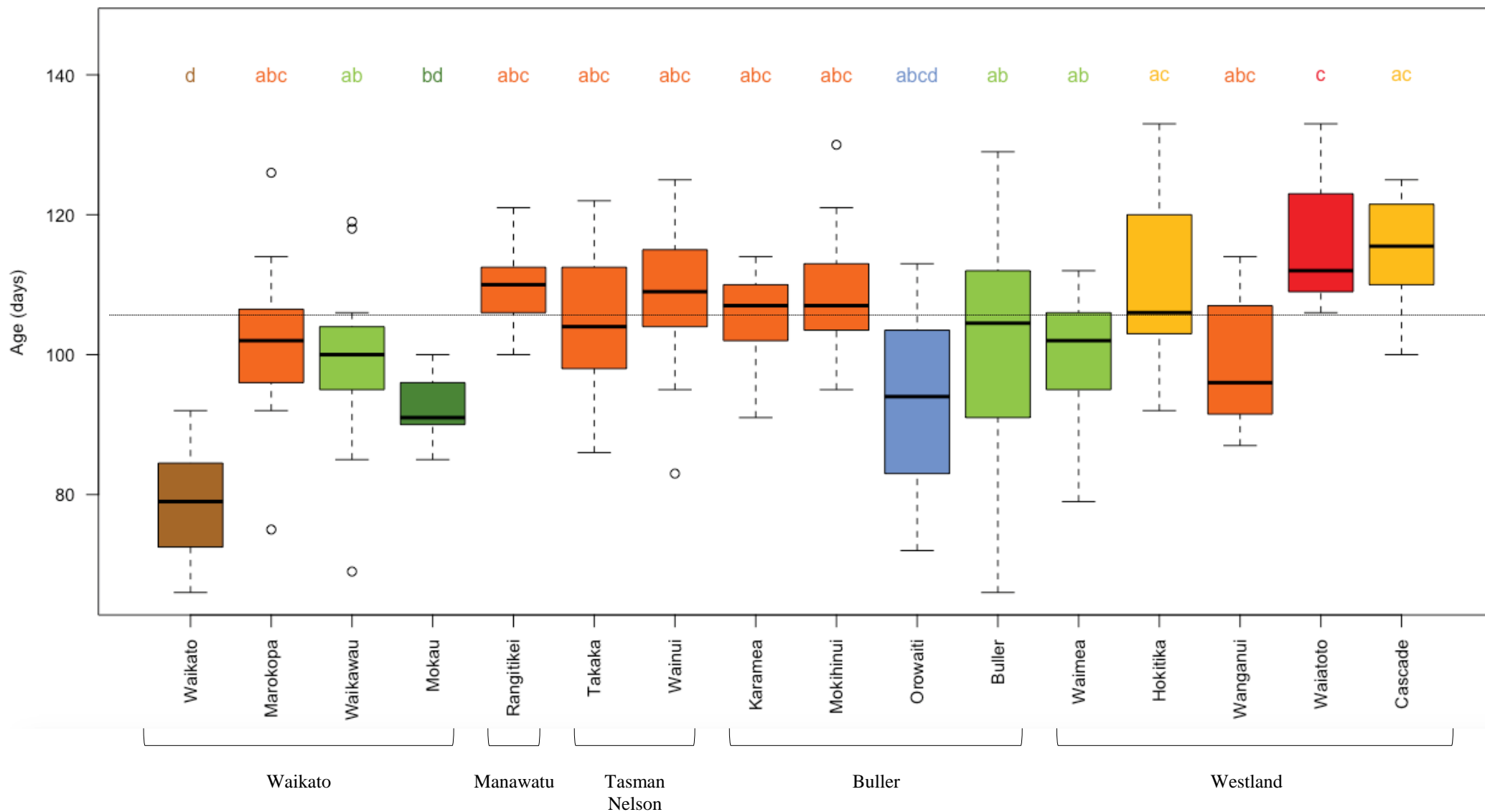
The age at migration of banded kōkopu whitebait showed little variation in the Tasman-Nelson region. Banded kōkopu post-larvae entering the Takaka and Wainui River during October 2015 did not differ significantly in age ( $F_{1,29} = 0.97$ ,  $p = 0.333$ ).

*Buller*

In October 2015, the age at migration of banded kōkopu whitebait entering the four rivers in Buller did not differ significantly between rivers ( $F_{3,41} = 1.86, p = 0.151$ ).

*Westland*

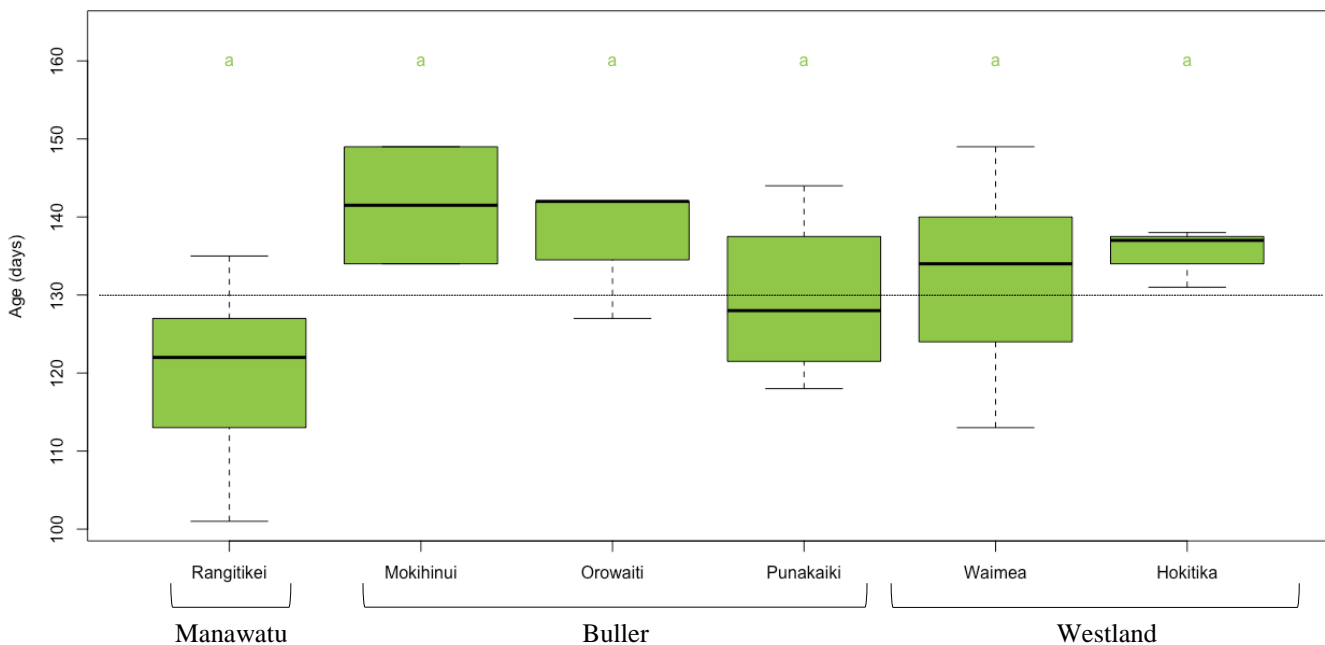
There were significant differences between rivers in Westland in the ages of post-larval banded kōkopu ( $F_{4,48} = 6.86, p < 0.05$ ). Whitebait entering the Cascade ( $\bar{x} \pm \text{SE age: } 114.9 \pm 3.0 \text{ d}$ ) and Waiatoto Rivers ( $115.4 \pm 2.2 \text{ d}$ ) were older than those entering the Wanganui River ( $99.1 \pm 3.8 \text{ d}$ ).



**Figure 4.2.** Age at migration of banded kōkopu whitebait (*G. fasciatus*) entering 16 rivers within New Zealand during October 2015. Boxes represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values. Different letters above boxes indicate rivers that are significantly different (Tukey's HSD,  $p < 0.05$ ). Dotted line denotes the overall mean age.

#### 4.4.4 Age of giant kōkopu and shortjaw kōkopu whitebait

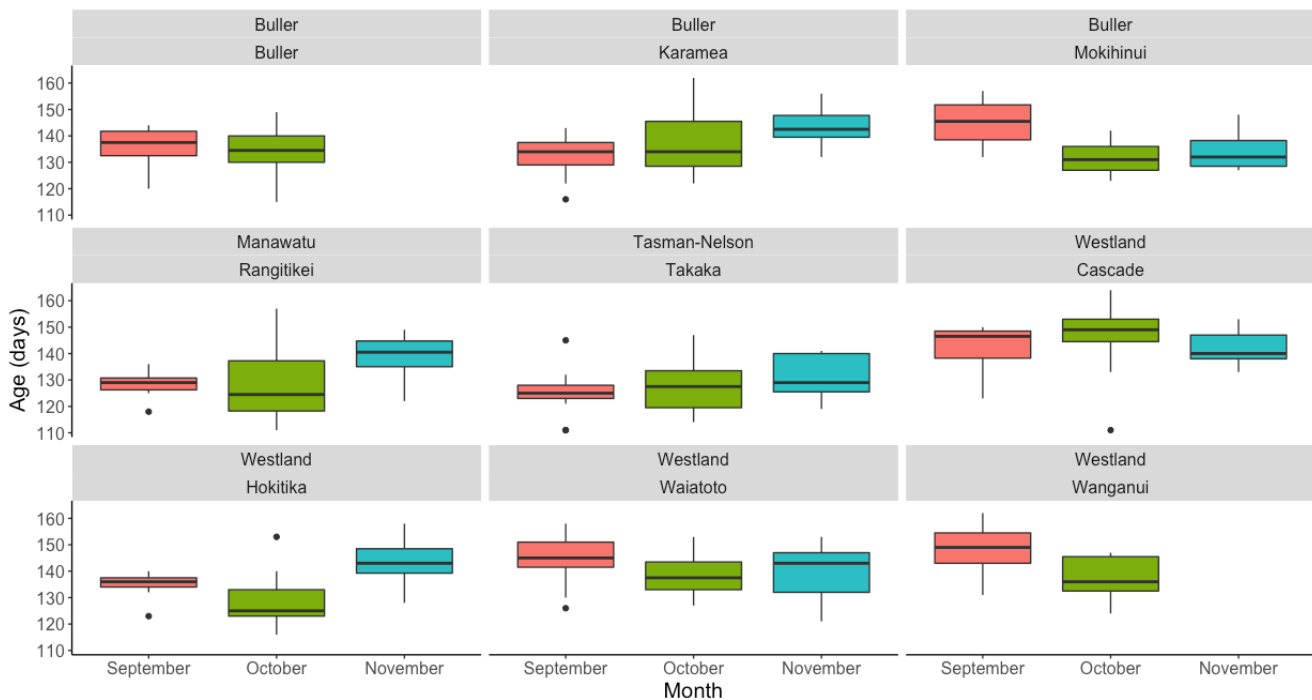
The mean age at migration of giant kōkopu whitebait was 130.9 days. Sample means ranged from 120 days to 141.5 days, with overall ages ranging from 101 days to 149 days. In November and December 2015, there was no significant difference between rivers in the mean age of giant kōkopu whitebait ( $F_{5,24} = 1.925, p = 0.127$ ; Fig. 4.3). The two individuals used to determine the age at migration of shortjaw kōkopu were collected from Orowaiti and Buller Rivers (Buller). These individuals were genetically confirmed as shortjaw kōkopu (*G. postvectis*) with the average age at migration being 152 days old.



**Figure 4.3.** Age at migration of giant kōkopu whitebait (*G. argenteus*) in six rivers of New Zealand during November and December 2015. Boxes represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values. Dotted line denotes overall mean.

#### 4.4.5 Temporal variation in age of kōaro whitebait

There was no consistent temporal pattern across rivers in the age at migration of kōaro whitebait (Fig. 4.4). Within the Buller region, kōaro whitebait entering the Karamea River ( $F_{2,41} = 4.79, p < 0.05$ ; Fig. 4.4) were younger in September ( $\bar{x} \pm \text{SE age: } 133.2 \pm 1.9 \text{ d}$ ) than in November ( $143.1 \pm 1.9 \text{ d}$ ). The opposite pattern was seen in the Mokihinui River ( $F_{2,23} = 7.796, p < 0.05$ ; Fig. 4.4) with whitebait entering the river towards the end of the settlement period being younger. The only other river with significant differences between months in age at migration was the Hokitika River ( $F_{2,25} = 5.827, p < 0.05$ ; Fig. 4.4). Here, whitebait entering in October ( $\bar{x} \pm \text{SE age: } 129.3 \pm 3.8 \text{ d}$ ) were younger than those in November ( $143.6 \pm 3.3$ ).

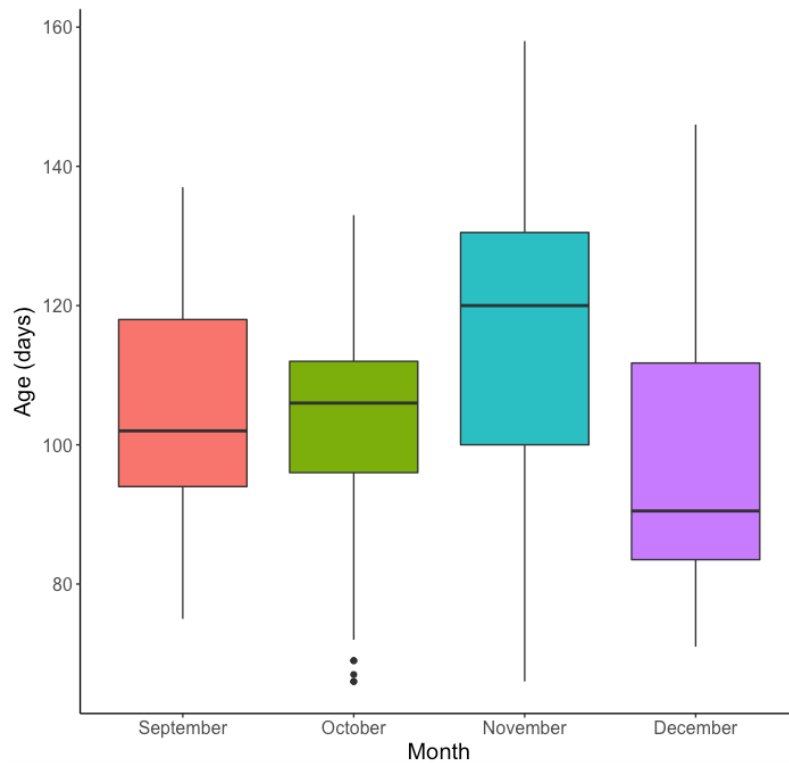


**Figure 4.4.** Age at migration of kōaro whitebait (*G. brevipinnis*) collected from nine rivers during September, October and November 2015. Boxplots represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values.



#### 4.4.6 Temporal variation in age of banded kōkopu whitebait

Of the sixteen rivers sampled, ten showed significant temporal differences in age at migration of banded kōkopu post-larvae, but there were few consistent patterns. Overall, banded kōkopu whitebait entering rivers in December were younger than those entering earlier in the settlement period ( $F_{3,339} = 7.65, p < 0.05$ ; Fig. 4.5).



**Figure 4.5.** Age at migration of kōaro whitebait (*G. brevipinnis*) collected in September, October, November and December 2015. Boxes represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values.

#### Waikato

There was no consistent temporal pattern in age of banded kōkopu entering rivers in the Waikato region (Fig. 4.6). In the Waikato River ( $F_{1,25} = 9.243, p < 0.05$ ; Fig. 4.6) banded kōkopu whitebait were older in September ( $\bar{x} \pm \text{SE}$  age:  $90.3 \pm 2.67$  d) than in October ( $79 \pm 2.48$  d). In the Marokopa River ( $F_{2,28} = 8.293, p < 0.05$ ; Fig. 4.6) banded kōkopu whitebait were older in October ( $101.9 \pm 3.0$  d) than in September ( $93.1 \pm 1.7$  d) or November ( $76.0 \pm 3.0$  d). In the Mokau River ( $F_{2,18} = 9.718, p < 0.05$ ; Fig. 4.6) banded kōkopu whitebait were significantly younger in October ( $95.57 \pm 2.10$  d) and November ( $77.50 \pm 3.50$  d) than in September ( $103.75 \pm 2.92$ ).

### *Manawatu*

The Rangitikei River did not follow the same trends as rivers within the Westland region. Significant differences in age ( $F_{2,36} = 4.191, P < 0.05$ ; Fig. 4.6) were present between October ( $\bar{x} \pm SE$  age:  $109.42 \pm 1.64$  d) and November ( $99 \pm 2.60$  d) with an overall decrease across the settlement period.

### *Tasman- Nelson*

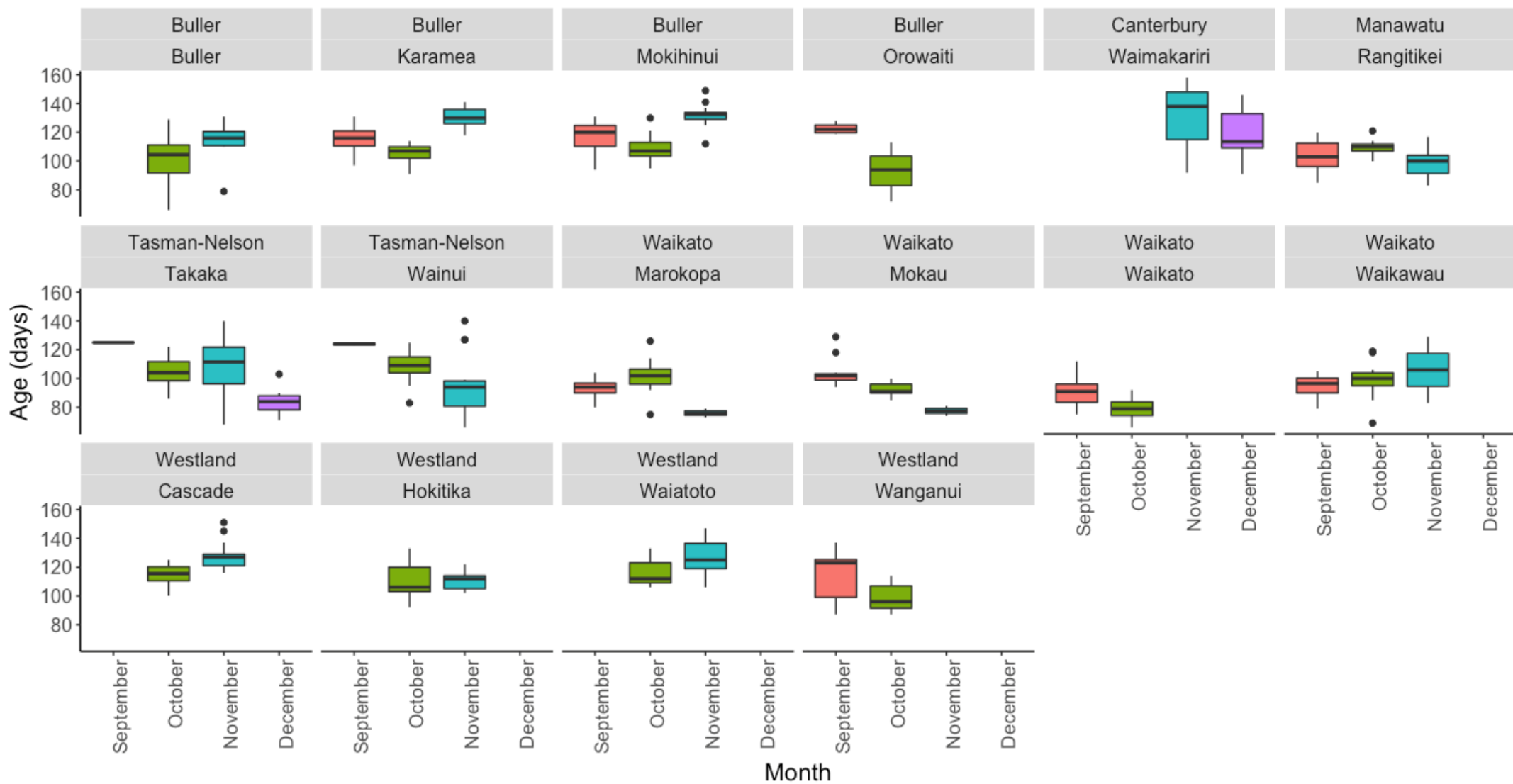
The overall trend in this region was a decrease in the age of banded kōkopu whitebait in later months of the settlement period. In the Takaka River ( $F_{2,37} = 8.186, p < 0.05$ ; Fig. 4.6), banded kōkopu whitebait in samples collected in September (125 d), October ( $104.9 \pm 2.4$  d) and November ( $109.3 \pm 5.1$  d) were all significantly older than fish sampled during December ( $84.1 \pm 2.9$  d).

### *Buller*

The ages of banded kōkopu whitebait entering rivers in the Buller region were highly variable. In most rivers (where sample sizes allowed comparisons) post-larvae were younger in October than in September and older in November than in October. For example, banded kōkopu whitebait entering the Karamea River ( $F_{2,40} = 34.19, p < 0.05$ ; Fig 4.6) in September ( $\bar{x} \pm SE$  age:  $115.2 \pm 2.4$  d) were older than whitebait in October ( $105.2 \pm 1.9$  d) which were in turn younger than whitebait in November ( $130.0 \pm 2.0$  d).

### *Westland*

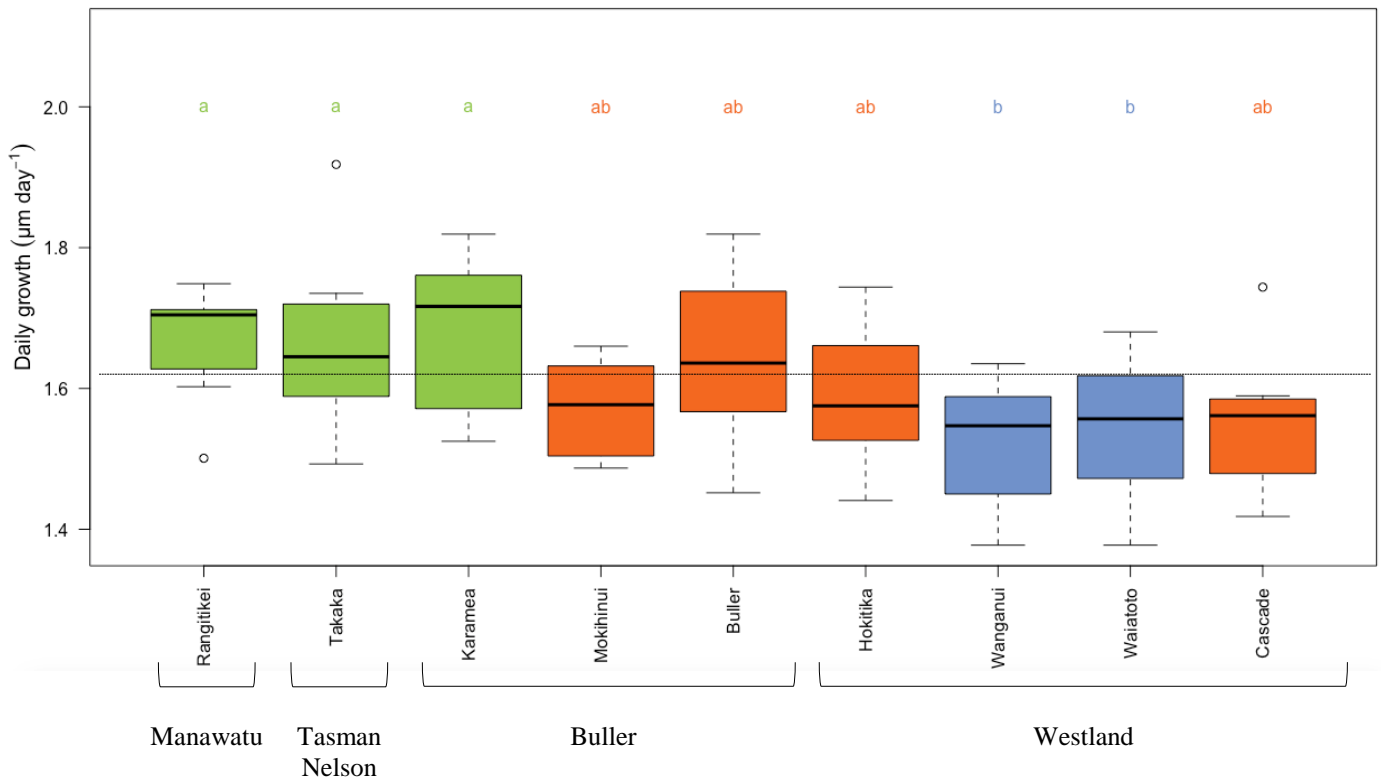
Sample sizes limited the comparisons that could be made in this region, but banded kōkopu whitebait entering the Cascade River ( $F_{1,19} = 10.11, p < 0.05$ ; Fig. 4.6) and Waitatoto River ( $F_{1,25} = 7.614, p < 0.05$ ; Fig. 4.6) were younger in October than in November.



**Figure 4.6.** Age at migration of banded kōkopu whitebait (*G. fasciatus*) from 16 rivers during September, October, November and December 2015. Boxes represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values.

#### 4.4.7 Spatial variation in growth rate of kōaro whitebait

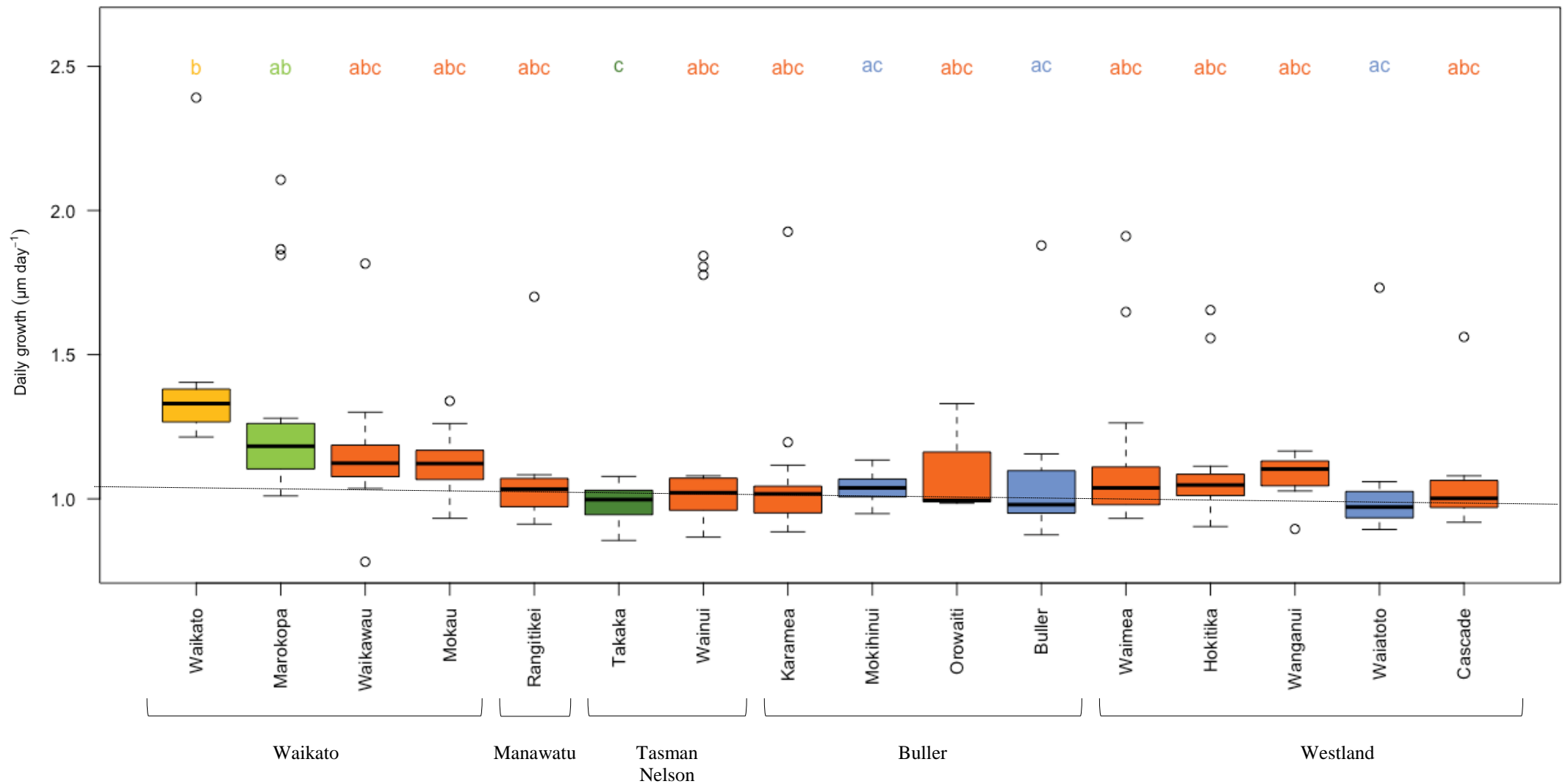
The average daily pelagic growth of kōaro whitebait entering rivers in New Zealand displayed strong spatial variation ( $F_{8,100} = 4.66, p < 0.05$ ; Fig. 4.7). In September 2015, kōaro whitebait entering rivers at higher latitudes had lower average daily pelagic growth than kōaro whitebait entering rivers at lower latitudes.



**Figure 4.7.** Daily pelagic growth rate of kōaro whitebait (*G. brevipinnis*) entering nine rivers in September 2015. Boxes represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values. Different letters above boxes indicate rivers that are significantly different (Tukey's HSD,  $p < 0.05$ ). Dotted line denotes overall mean.

#### 4.4.8 Spatial variation in growth rate of banded kōkopu whitebait

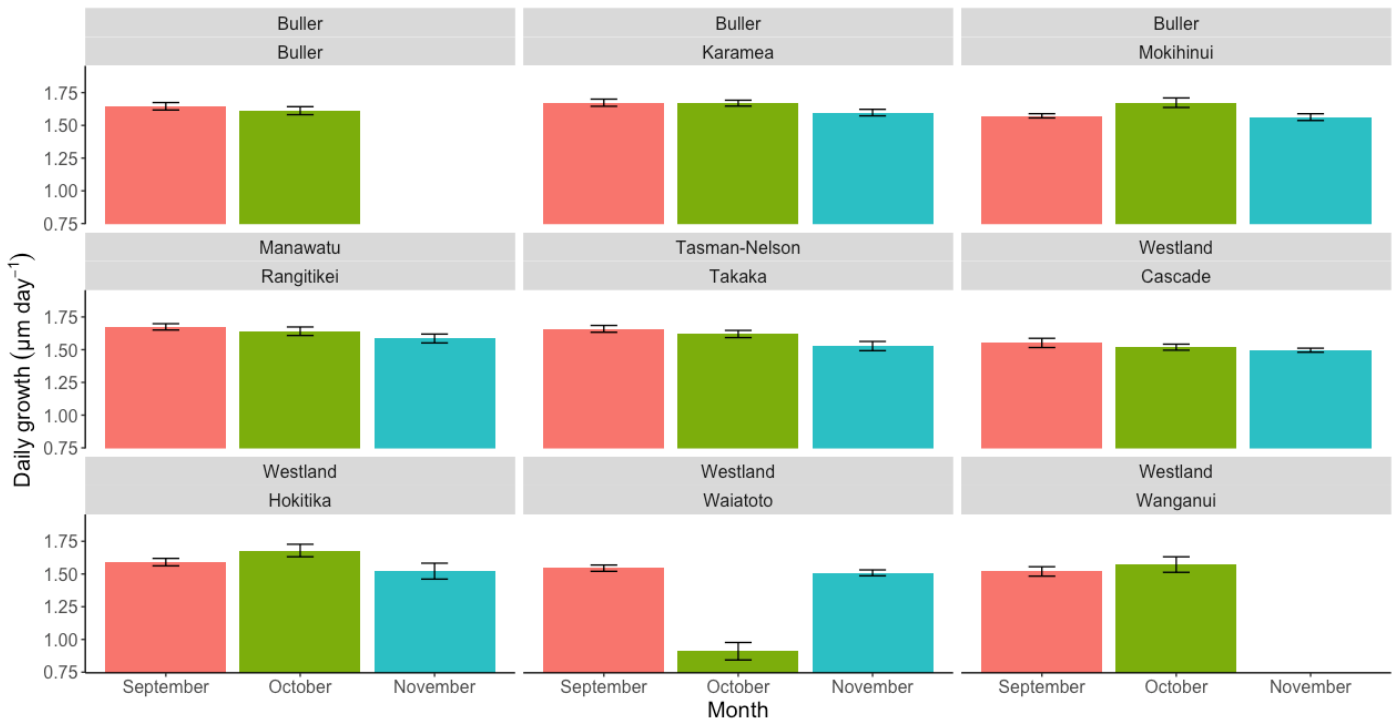
Banded kōkopu post-larvae also displayed spatial variation in average daily pelagic growth rates ( $F_{15,176} = 2.531, p < 0.05$ ; Fig. 4.8). Post-larvae entering rivers at higher latitudes had lower average daily growth rates than those entering rivers at lower latitudes. Banded kōkopu whitebait entering the Waikato River ( $\bar{x} \pm \text{SE growth: } 1.41 \pm 0.09 \mu\text{m d}^{-1}$ ) had significantly higher daily growth rates than banded kōkopu whitebait entering the Rangitikei ( $1.07 \pm 0.06 \mu\text{m d}^{-1}$ ), Takaka ( $0.98 \pm 0.02 \mu\text{m d}^{-1}$ ), Karamea ( $1.08 \pm 0.07 \mu\text{m d}^{-1}$ ), Mokihinui ( $1.04 \pm 0.01 \mu\text{m d}^{-1}$ ), Buller ( $1.06 \pm 0.07 \mu\text{m d}^{-1}$ ), and Waiaototo Rivers ( $1.03 \pm 0.06 \mu\text{m d}^{-1}$ ) in October 2015.



**Figure 4.8.** Daily pelagic growth rate of banded kōkopu (*G. fasciatus*) whitebait entering 16 rivers during October, 2015. Boxes represent median, lower and upper quartiles (25% and 75%) and minimum and maximum values. Different letters above boxes indicate rivers that are significantly different (Tukey's HSD,  $p < 0.05$ ). Dotted line denotes overall mean.

#### 4.4.9 Temporal variation in growth rate of kōaro whitebait

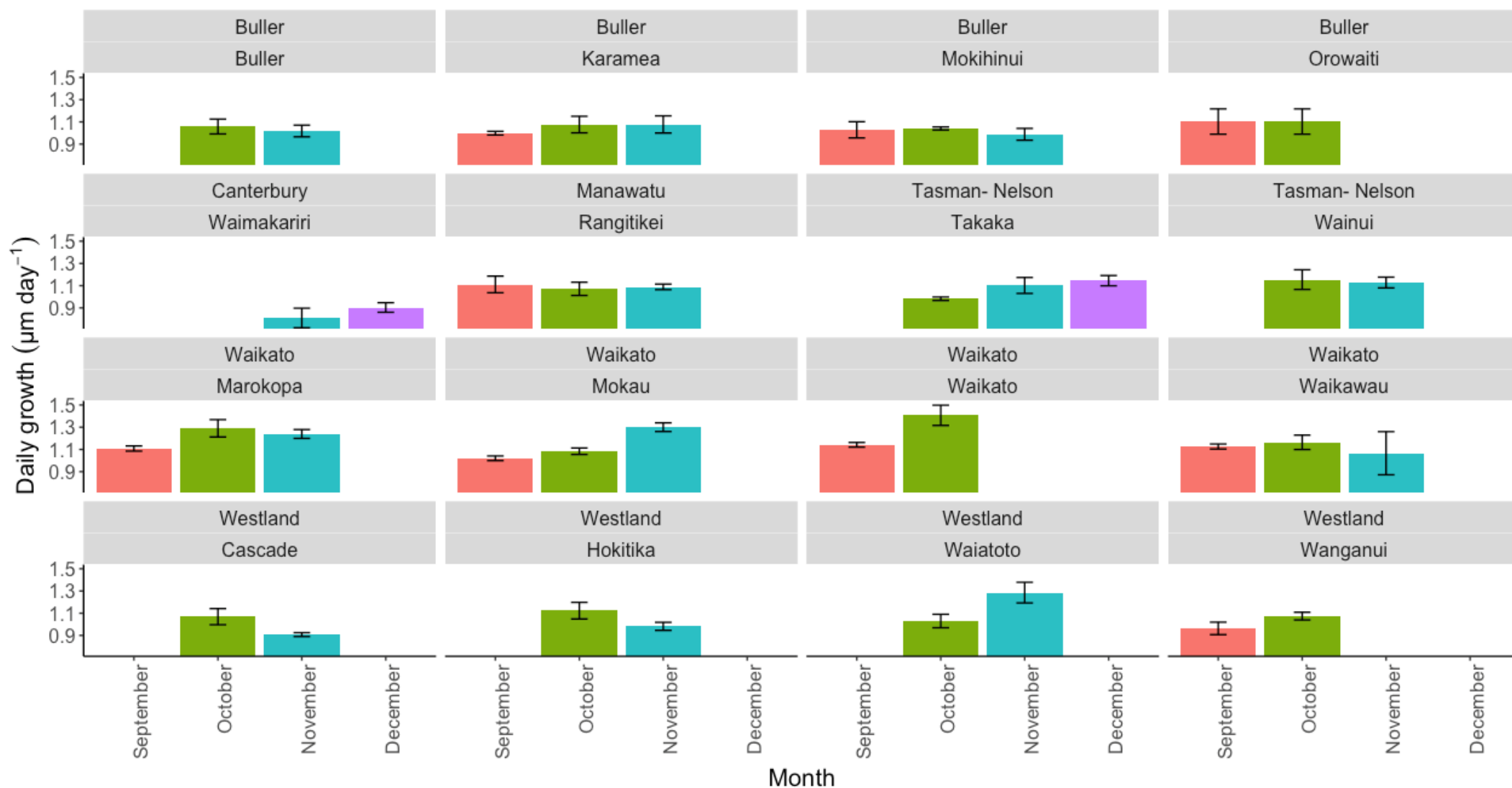
Of the nine rivers where sampling allowed a comparison of temporal variation in average daily pelagic growth of kōaro whitebait, only three showed significant differences among months and there was no consistent pattern. In the Waiatoto River ( $F_{2,39} = 69.11, p < 0.05$ ; Fig. 4.9) average daily growth rates of kōaro whitebait were significantly lower in October ( $0.91 \pm 0.07 \mu\text{m d}^{-1}$ ) than in September ( $1.54 \pm 0.02 \mu\text{m d}^{-1}$ ) or November ( $1.51 \pm 0.02 \mu\text{m d}^{-1}$ ). In the Takaka River ( $F_{2,33} = 4.07, p < 0.05$ ; Fig. 4.9) average daily growth rates decreased significantly between September ( $1.66 \pm 0.03 \mu\text{m d}^{-1}$ ) and November ( $1.53 \pm 0.04 \mu\text{m d}^{-1}$ ). Finally, kōaro whitebait entering the Mokihiui River ( $F_{2,23} = 5.20, p < 0.05$ ; Fig. 4.9) during September ( $1.57 \pm 0.02 \mu\text{m d}^{-1}$ ) had significantly lower average daily growth than whitebait entering during October ( $1.67 \pm 0.04 \mu\text{m d}^{-1}$ ).



**Figure 4.9.** Mean ( $\pm$  SE) daily pelagic growth rate of kōaro whitebait (*G. brevipinnis*) entering nine rivers during September, October and November 2015.

#### **4.4.10 Temporal variation in growth rate of banded kōkopu whitebait**

Of the 16 rivers where sampling allowed a comparison of temporal variation in average daily pelagic growth of banded kōkopu whitebait, only five rivers within two regions showed significant differences among months, and there was no consistent pattern. In the Waikato region, the average daily growth rate of banded kōkopu post-larvae entering the Waikato River ( $F_{1,25} = 9.86, p < 0.05$ ; Fig. 4.10) and the Mokau River ( $F_{2,18} = 12.66, p < 0.05$ ; Fig. 4.10) increased significantly from September onwards. In Westland, a similar pattern was found for banded kōkopu whitebait in the Waikatoto River ( $F_{1,25} = 5.15, p < 0.05$ ; Fig. 4.10) with whitebait entering in November ( $1.29 \pm 0.09 \mu\text{m d}^{-1}$ ) having higher growth rates than those entering in October ( $1.03 \pm 0.06 \mu\text{m d}^{-1}$ ). However, the opposite pattern was seen in the Hokitika ( $F_{1,14} = 1.51, p < 0.05$ ; Fig. 4.10) and Cascade Rivers ( $F_{1,19} = 7.15, p < 0.05$ ; Fig. 4.10) with the average daily growth of whitebait entering during November being significantly lower than those entering during October.

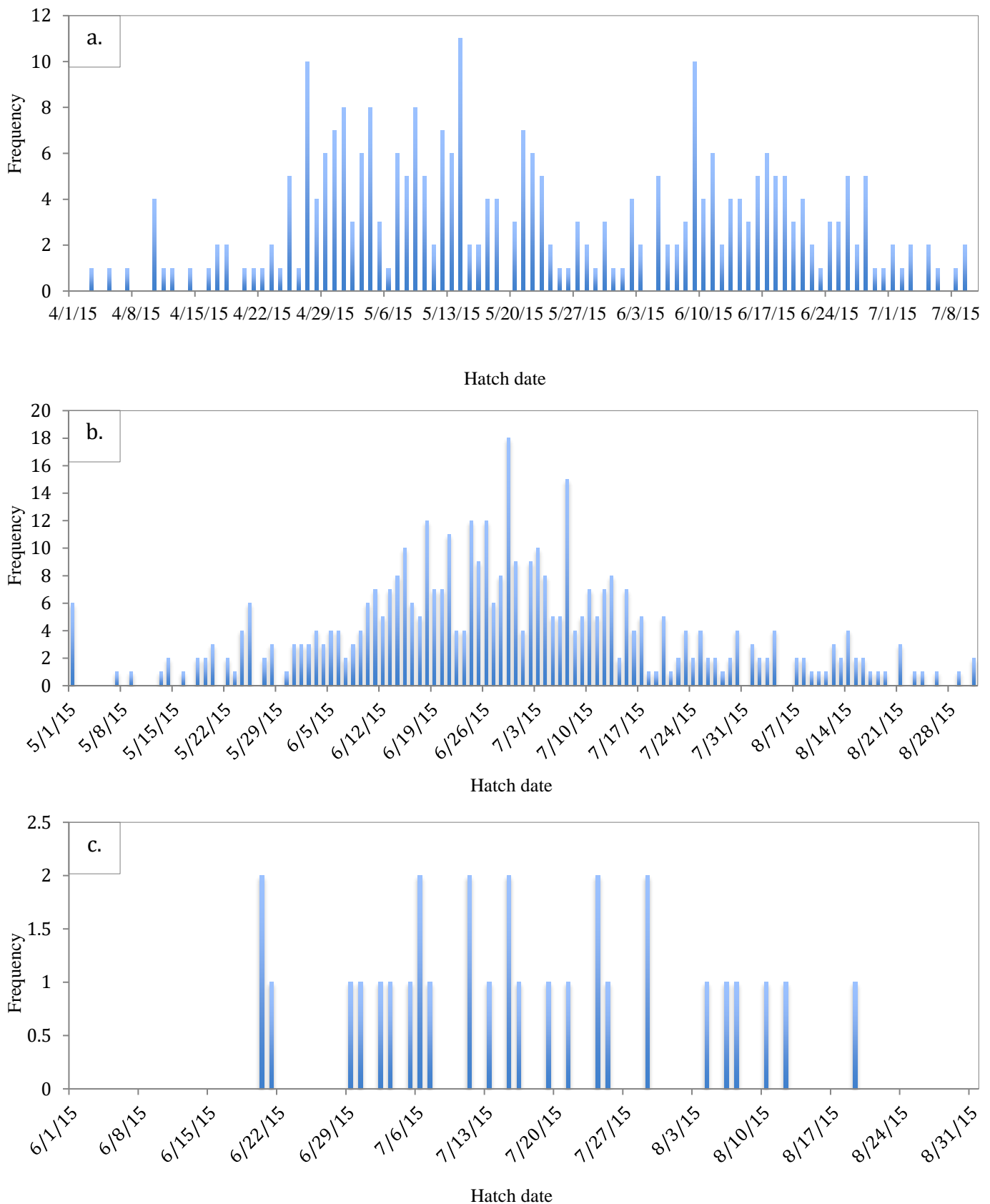


**Figure 4.10.** Mean (± SE) daily pelagic growth rate of banded kōkopu whitebait (*G. fasciatus*) entering 16 rivers during September, October, November and December 2015.



#### **4.4.11 Hatch date distribution of kōaro, banded kōkopu and giant kōkopu**

The hatch date distributions of kōaro, banded kōkopu and giant kōkopu differed in shape and breadth. Kōaro whitebait had a broad hatch date distribution with major peaks in spawning during mid-May and mid-June (Fig 4.11a). From the kōaro whitebait sampled, 42% hatched during May and 35% hatched in June. Banded kōkopu whitebait had a more concentrated unimodal hatch distribution than kōaro (Fig 4.11b). From the banded kōkopu whitebait sampled 46% hatched in June and 32% hatched in July. Giant kōkopu whitebait hatched from late June to mid-August. Most giant kōkopu hatched in July (63%).



**Figure 4.11.** Hatch date distribution of **a.** kōaro (*G. brevipinnis*) whitebait from 10 rivers in New Zealand, samples collected during September, October and November 2015 (n=296). **b.** Banded kōkopu (*G. fasciatus*) from 19 rivers in New Zealand collected from September through to December 2015 (n=446). **c.** Giant kōkopu (*G. argenteus*) from 6 rivers of New Zealand from November and December (n=30). Hatch dates were derived from age estimates from otoliths.

## 4.5 Discussion

Overall, kōaro, banded kōkopu and giant kōkopu whitebait all exhibited large variation in age at migration. For post-larval kōaro entering New Zealand rivers, mean ages ranged from 125.4 to 170.5 d with an overall mean age of 138.3 d. Banded kōkopu were considerably younger than kōaro with mean ages ranging from 46 to 131.9 d and an overall mean age of 106.2 d. Giant kōkopu mean ages ranged from 120 to 141.5 d with an overall mean age of 130.9 d. Although limited by sample size ( $n=2$ ), shortjaw kōkopu were on average 152 days old at migration.

My results show considerably more variation in age than studies such as McDowall *et al.* (1994) and McDowall and Kelly (1999). These studies found whitebait ages to range from 110-155 d for kōaro, 93-128 d for banded kōkopu, 113-137 d for giant kōkopu and 120-136 d for shortjaw kōkopu. Although my study found larger variation in age, it was in agreement with earlier studies with similar trends between species: kōaro and shortjaw kōkopu whitebait were on average older than banded kōkopu and giant kōkopu whitebait.

Comparisons between all rivers sampled revealed a large latitudinal gradient in the age at migration for kōaro and banded kōkopu. For both species, fish entering rivers at lower latitudes (North Island) were younger at migration than those entering rivers at higher latitudes (South Island). These results were consistent with results for the most abundant whitebait species, īnanga (Section 2.5.2). This latitudinal gradient coupled with the broader latitudinal span of samples in my study is likely driving the higher levels of age variation seen in my study in comparison to McDowall *et al.* (1994). McDowall *et al.* (1994) sampled rivers confined to only the North Island for species such as banded kōkopu. In my study, kōaro whitebait from the Wanganui River in Westland had an average age of 148.1 d in September. McDowall *et al.* (1994) only aged 10 fish from Westland (Okarito) and these were collected in late November. Given the trend that the average age of kōaro whitebait entering some Westland rivers decreases in later months, it is unsurprising that my study recorded significantly older kōaro whitebait than McDowall *et al.* (1994). My study recorded banded kōkopu whitebait from the Cascade River in Westland that had an average age of 114.9 d in September. McDowall *et al.* (1994) did not age any banded kōkopu whitebait from South Island waterways.

For kōaro and banded kōkopu whitebait, a latitudinal gradient in average daily pelagic growth rate was recorded. For both species, average daily growth rates were higher for post-larvae entering rivers at lower latitudes, and growth rates were lower for post-larvae entering rivers in the higher latitudes of New Zealand. Banded kōkopu growth rates were on average lower than kōaro. These growth rate results are similar to those in a study by Egan (2017). Egan (2017) found that īnanga whitebait entering rivers in the Bay of Plenty had higher age-dependent growth rates than fish entering rivers in South Island regions.

Because the three whitebait species that could be analysed in this chapter (kōaro, banded kōkopu and giant kōkopu) exhibited similar latitudinal variations in age, it is likely that oceanic conditions within each region are driving similar responses in pelagic growth across the three species (Houde, 1989). Warmer water temperatures coupled with higher levels of production are most likely driving higher levels of growth and subsequently shorter larval pelagic durations in whitebait at lower latitudes. The suggestion that oceanic conditions such as sea surface temperature and productivity drive variation in traits of species is widely supported in the literature. Latitudinal changes in temperature are known to drive trait variability in other marine species (McLeod *et al.*, 2015, Lord, 2017) and some species of terrestrial plants (Matías and Jump, 2015).

Īnanga have a protracted hatch date distribution (Fig. 3.12) with peaks that coincide with the lunar cycle (Benzie, 1968). The spawning strategy of banded kōkopu and kōaro also involves terrestrial egg development, but in these species, hatching occurs after eggs are re-immersed due to flooding (Koehn and O'Connor, 1992). This form of egg re-immersion means that hatching in these species is less regular than the tidally-induced hatching of īnanga.

Banded kōkopu hatch dates had a unimodal distribution, whereas the hatch date distribution of kōaro was broader with a bimodal distribution. Hatching of giant kōkopu occurred from June through to August. These findings build on observations by McDowall *et al.* (1994) who estimated that the majority of banded kōkopu hatch in June, kōaro in early May, and giant kōkopu in mid-June. My results suggest that the majority of banded kōkopu hatch during late June/early July, and kōaro from early May to June.

## **Chapter 5: General Discussion**

### **5.1 Overview**

Traditionally, species with planktonic phases in their life history were considered to form demographically open metapopulations with high levels of gene flow (Sanford and Kelly, 2011). Only within the last decade has research begun to recognise the lack of connection between populations, giving rise to the concept of local adaptation in response to both spatial and temporal variation in oceanic conditions (oceanic features, temperature and food availability) (Levin, 2006). My study investigated possible spatial and temporal variations in early life history traits of the New Zealand whitebait fishery and its five constituent species. It described New Zealand-wide variation in early life history traits such as age at migration of post-larvae and pelagic growth, making comparisons between rivers, between regions and between months.

Overall, my study found that age at migration and daily pelagic growth in the three most abundant whitebait species īnanga, kōaro and banded kōkopu displayed large spatial variation. In northern regions of New Zealand, whitebait tended to be younger on average with higher average daily growth. In southern regions, whitebait were older and had grown more slowly while in their larval phase. There was also some variation between east and west coasts of the South Island with older whitebait on the east coast compared to those entering rivers at similar latitudes on the West Coast. In many cases, regions that had coastal waters characterised by large annual amplitudes in sea surface temperature or large spring blooms of productivity also had younger whitebait with higher larval growth rates.

### **5.2 Spatial variation in age and growth**

This study is the first to make broad-scale spatial comparisons of age and growth of whitebait species. Age ranges for each whitebait species were greater than those reported in other studies such as McDowall, Mitchell and Brothers (1994). This is likely due to the inclusion of considerably more rivers (26) and individuals ( $n = 1,567$ ) across a greater latitudinal span. However, age at migration comparisons between the species still reflected the same pattern reported in previous studies: īnanga whitebait were the oldest at migration and banded kōkopu whitebait were substantially younger than the other species (McDowall et al., 1994).

Īnanga whitebait had the highest average daily growth rate. Īnanga growth rates were very similar to those recorded for whitebait of the same species in southern Australia (Barbee *et al.*, 2011) that had developed in coastal waters with similar temperature and productivity characteristics. Kōaro larval growth rates were lower than Īnanga, but banded kōkopu average daily pelagic growth rates were considerably lower again and less variable. These are the first interspecific comparisons of daily pelagic growth rates that have been documented for New Zealand whitebait.

The large spatial variations in age at migration and daily pelagic growth rates suggest some form of partitioning occurring between regions and in some cases rivers with regions. Natal homing can be ruled out as a fine-scale driver of partitioning for Īnanga as a study conducted by Hickford and Schiel (2016) found they formed regional larval pools with ‘leaky borders’ and dispersing Īnanga larvae very rarely returned to their natal stream. Instead of natal homing, the spatial variations in age at migration and daily pelagic growth rates are most likely caused by local adaptation to fine-scale oceanic conditions (Houde, 1989, Sanford and Kelly, 2011).

In the last decade there has been an increased recognition of local adaptation occurring in marine populations (Palumbi, 2004). The oceanic conditions that drive this local adaptation include water temperature (Houde, 1989), food availability (productivity) (Searcy and Sponaugle, 2001) and larval mortality as a result of starvation and predation (Leggett and Deblois, 1994). Recognition of local adaptation has been partially responsible for changing the long-held paradigm that all species with pelagic larvae form well-mixed meta-populations (Levin, 2006).

In New Zealand, localised oceanic conditions and therefore local adaptation are likely a result of the complex bathymetry, topography and currents that surround New Zealand (Murphy *et al.*, 2001, Sanford and Kelly, 2011). New Zealand coastal waters have a strong latitudinal gradient in temperature (Chiswell, 1994, Uddstrom and Oien, 1999) that coincides with the spatial variation in age and growth that is seen in the majority of the whitebait species. Warmer temperatures have been linked to increased growth, and food consumption which has found to decrease pelagic larval duration in many species of fish (Houde, 1989, Levin, 2006). It is therefore suggested that the latitudinal gradient seen in age and growth of whitebait is at least partially driven by the latitudinal gradient seen in sea surface temperature.

Sea surface temperature (SST) shows little variation between points at the same latitude on the east and west coast of New Zealand. As such, SST alone is unlikely to produce the oceanic conditions that cause whitebait on the east coast (Canterbury) to be older and slower growing than those entering rivers at similar latitudes on the West Coast. However, spatial variation in productivity may drive this east/west differentiation (Keller and Klein-MacPhee, 2000, Rissik and Suthers, 2000). Variation in productivity has been shown to drive ecologically significant variability in populations via influences on prey abundance and growth, secondary production and consumer growth (Menge, 2000). Productivity in most of New Zealand's coastal waters tends to follow a 'spring bloom cycle', but productivity on the West Coast of the South Island is higher than east coast regions because of coastal upwelling (Menge *et al.*, 2003, Schiel, 2004).

### **5.3 Temporal variation in age and growth**

The pelagic environment that larval fish are exposed to is not static with defined seasonal (and longer-scale) variations in temperate and polar oceans (Levitus, 1986, Levitus *et al.*, 2000). Some regions have large seasonal fluctuations in water temperature, productivity and pH, whereas other areas can display very weak fluctuations (Sanford and Kelly, 2011). Seasonal fluctuations in physical parameters are common in New Zealand coastal waters and are recognised drivers of temporal differentiation in marine populations (e.g., Jones, 1988).

Of the five whitebait species, īnanga had the most apparent temporal variability in age at migration and growth. This was most likely a result of more comprehensive sampling of īnanga whitebait (samples from all rivers contained īnanga whitebait). Kōaro and banded kōkopu whitebait had less temporal variability in age at migration and daily pelagic growth rate, but this was likely due to sampling restrictions.

The relationship between age at migration and daily pelagic growth across spatial and temporal scales for the majority of the whitebait species suggests warmer/productive oceanic environments allow individuals to grow faster and leave the pelagic environment sooner. Conversely, cooler and/or less productive environments restrict growth rates and cause longer pelagic larval durations. For most of the whitebait species these older, slower growing fish are also larger at migration (Yungnickel, 2017).

#### **5.4 What are the consequences of the observed variability in early life history traits?**

Fisheries scientists were the first to hypothesise about the consequences of different early life history growth trajectories. Hjort (1914) formulated the “critical period” hypothesis, and stated that newly hatched larvae that “did not succeed in finding the very special food they wanted would die from hunger” (Hjort, 1926). This hypothesis was later refined into the match–mismatch hypothesis by Cushing (1973). The match–mismatch hypothesis suggests that larval fish that hatch near the peak abundance of their zooplankton prey will survive better (Cushing, 1990).

Hjort's (1914) concept of a “critical period” still dominates fisheries recruitment science. More recently it has been complemented by other hypotheses that seek to explain how food availability in the planktonic environment can be causally linked to survival. The “bigger is better” hypothesis (Houde, 1987; Litvak and Leggett, 1992) is based on the observation that initial predation rates of larval fish are extreme but that they decline rapidly as larval fish become larger (McGurk, 1986; Houde, 1987). This lead to the closely related “stage duration” hypothesis. Rather than focusing explicitly on size, it concentrates on the period spent in smaller more vulnerable size-classes; with increased growth rates, this period is shortened and survival is higher (Shine, 1978; Houde, 1997). Lastly, the “growth-selective predation” hypothesis, was based on observations that slow-growing larvae were more likely to be eaten because starvation reduced swimming performance and anti-predator behaviours (Takasuka *et al.*, 2003). The common assumption made by the three hypotheses is that favourable food conditions will increase pelagic growth rate, which in turn will have a positive effect on the survival of larval fish.

With these hypotheses in mind, it is clear that larval whitebait developing in coastal environments at lower latitudes in New Zealand, such as the Bay of Plenty, benefit from a warmer, more productive, pelagic environment that allows faster growth. More rapid development allows these whitebait to leave the pelagic environment sooner and increases their chances of survival.

#### **5.5 Hatch date distributions**

The whitebait life cycle is based around a winter at sea (hatching and pelagic development) followed by migration and further development in freshwater (McDowall and Eldon, 1980). Īnanga whitebait hatched substantially sooner than the other species with pulses of hatching



occurring from January until August and the majority of īnanga hatched during May. Kōaro whitebait also had a broad hatch distribution with hatching occurring on multiple dates between April and July and the majority hatching during May. Banded kōkopu whitebait had a more concentrated hatch distribution with most hatching occurring in June and July. Giant kōkopu whitebait hatched between July and August. These hatch dates are considerably broader than those found by McDowall *et al.* (1994) but this is likely a result of the more comprehensive temporal sampling in my study.

From the hatch date distributions it is clear that each of the whitebait species has adapted a different spawning strategy. Īnanga have a primarily semelparous reproductive strategy (see Stevens *et al.* 2016) where they produce a large number of small eggs (McDowall, 1968). The wide distribution of hatching pulses indicates a protracted spawning season that is typical of a bet-hedging strategy to produce multiple cohorts. The production of multiple cohorts is a way to reduce intraspecific competition and increase the chance that offspring will be exposed to favourable oceanic conditions (Houde, 1989). This strategy is also seen in kōaro who have extending hatching over multiple months.

## 5.6 Future research

Several questions with respect to spatial and temporal variability in the early life history traits of the species that comprise the whitebait fishery have been answered in this study. It is clear that each of the five species that make up the fishery is not characterized by one large meta-population and that spatial and temporal changes in oceanic conditions around New Zealand are responsible for at least some of the variation seen within post-larvae.

Going forward, it is crucial that future research is conducted at least at regional scales in order to incorporate the large variability seen here and prevent incorrect generalisations being made about each species (Barbee *et al.*, 2011). This suggestion is supported by other studies that incorporated a broad spatial component to sampling (Egan, 2017, Yungnickel, 2017) and who also found regional variation in species composition, morphology, growth and age.

Sample sizes in this study have exceeded those in previous research that has focused on early life history traits (McDowall *et al.*, 1994, Barbee *et al.*, 2011). Although 1567 fish were aged, the majority of these were the most abundant whitebait species, īnanga (McDowall, 1968). From studies such as Yungnickel (2017) it is apparent that composition of species in the

whitebait catch varies, but also that species identification is difficult. The use of genetic testing is imperative to distinguish some species. Due to the heterospecific nature of the fishery, future research should focus on the less abundant species in the whitebait catch such as kōaro, shortjaw kōkopu and giant kōkopu.

In my study, temporal comparisons were made between whitebait entering rivers in September, October and November. Whitebait migrations peak during these spring months, but post-larvae enter rivers in most regions of New Zealand throughout the year albeit in very low numbers. (e.g., Barbee *et al.*, 2011) sampled post-larvae in southern Australia between September and January and found greater differences than my study in the age and growth of īnanga whitebait. Expanding the temporal sampling of whitebait beyond that of my study would provide a broader picture of how early life history traits adapt to more extreme oceanic conditions. With the threat of substantial changes to oceanic conditions through climate change, an understanding of the consequences of more extreme oceanic conditions on larval growth and survival will be essential to plan future changes to the management of the whitebait fishery (Deutsch *et al.*, 2008, Chen *et al.*, 2011).

## 5.7 Summary

From this study is apparent that the New Zealand whitebait fishery is not comprised of a single meta-population. Spatial differences in oceanic conditions drive local adaptation and variability in early life history traits. Key findings included establishing a strong latitudinal gradient in the age and larval growth of the three most common whitebait species: at lower latitudes, whitebait were younger with higher average daily growth rates. For many rivers, the age of whitebait did not decrease across the fishing as previous studies have suggested. Derived hatch date distributions suggest that the spawning season of most of the whitebait species is more protracted than previously thought.

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## Appendix

CODE	SPECIES	UNIQUE#	EXTRACTED	TRAY	LOCATION	L or R	DATE
Takaka							
TASNEL_TAKAKA_SEAN_020915_41	koaro	7649					
TASNEL_TAKAKA_SEAN_020915_42	koaro	7650					
TASNEL_TAKAKA_SEAN_020915_43	koaro	7651					
TASNEL_TAKAKA_SEAN_020915_44	koaro	7652					
TASNEL_TAKAKA_SEAN_020915_45	koaro	7653					
TASNEL_TAKAKA_SEAN_020915_46	koaro	7654					
TASNEL_TAKAKA_SEAN_020915_47	koaro	7655					
TASNEL_TAKAKA_SEAN_020915_48	koaro	7656					
TASNEL_TAKAKA_SEAN_020915_49	koaro	7657					
TASNEL_TAKAKA_SEAN_020915_50	koaro	7658					
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TASNEL_TAKAKA_SEAN_020915_52	koaro	7660					
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TASNEL_TAKAKA_SEAN_020915_54	koaro	7662					
TASNEL_TAKAKA_SEAN_020915_55	koaro	7663					
TASNEL_TAKAKA_SEAN_020915_56	koaro	7664					
TASNEL_TAKAKA_SEAN_020915_57	koaro	7665					
TASNEL_TAKAKA_SEAN_020915_58	koaro	7666					
TASNEL_TAKAKA_SEAN_020915_59	koaro	7667					
TASNEL_TAKAKA_SEAN_020915_60	koaro	7668					
TASNEL_TAKAKA_SEAN_020915_61	koaro	7669					
TASNEL_TAKAKA_SEAN_020915_62	koaro	7670					
TASNEL_TAKAKA_SEAN_020915_63	koaro	7671					
TASNEL_TAKAKA_SEAN_020915_64	koaro	7672					
TASNEL_TAKAKA_SEAN_020915_65	koaro	7673					
TASNEL_TAKAKA_SEAN_020915_66	koaro	7674					
TASNEL_TAKAKA_SEAN_020915_67	koaro	7675					
TASNEL_TAKAKA_SEAN_020915_68	koaro	7676					
TASNEL_TAKAKA_SEAN_020915_69	koaro	7677					
TASNEL_TAKAKA_SEAN_020915_70	koaro	7678					
TASNEL_TAKAKA_SEAN_020915_71	koaro	7679					
TASNEL_TAKAKA_SEAN_020915_72	koaro	7680					
TASNEL_TAKAKA_SEAN_020915_73	koaro	7681					
TASNEL_TAKAKA_SEAN_020915_74	koaro	7682					
TASNEL_TAKAKA_SEAN_020915_75	koaro	7683					
TASNEL_TAKAKA_SEAN_020915_76	koaro	7684					
TASNEL_TAKAKA_SEAN_020915_77	koaro	7685					
TASNEL_TAKAKA_SEAN_020915_78	koaro	7686					
TASNEL_TAKAKA_SEAN_020915_79	koaro	7687					
TASNEL_TAKAKA_SEAN_020915_80	koaro	7688					